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Overview of Studies on the Nutrient Status of Lake Ontario

D. R. S. Lean

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Lean, D. R. S. 1987. Overview of studies on the nutrient status of Lake Ontario. Can. J. Fish. Aquat. Sci. 44: 2042–2046.

Balancing human demands on the environment with the overall welfare of the biosphere is one of the greatest challenges facing society today. In lakes, the limits of use and abuse are set by biogeochemical processes. This issue integrates measurements of lake physics and nutrient availability with the response of the microbial community in Lake Ontario. Such information is vital to the understanding of factors affecting the base of the food chain and relates to the phosphorus abatement programs of the past 15 yr.

L'obtention d'un équilibre entre les pressions humaines sur l'environnement et le bon état global de la biosphère constitue un des plus grands défis auquel doit faire face la société contemporaine. En milieu lacustre, les processus biogéochimiques fixent les limites entre l'exploitation et la surexploitation. Il faut donc intégrer les quantifications des facteurs physiques lacustres et de la disponibilité des bioéléments aux réactions de la communauté microbienne dans le lac Ontario. De telles données sont essentielles à la compréhension des facteurs agissant à la base de la chaîne alimentaire et sont liées aux programmes de réduction du phosphore menés au cours des 15 dernières années.

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Environment Canada undertook a series of cruises on Lake Ontario in 1982 to assess the nutrient status of the lake. On behalf of the National Water Research institute, I was responsible for the Lake Ontario Nutrient Assessment Study (LONAS). This multidisciplinary seasonal study of nutrient dynamics included extensive investigations of physical processes but focused on the influence of phosphorus and nitrogen on algal growth and plankton composition as well as the transport rates between biological compartments. Concurrently, a 2-yr intensive surveillance program was conducted by the Water Quality Branch on the open waters of Lake Ontario in fulfillment of the requirements of the Great Lakes International Surveillance Plan (GLISP). Other investigations supported by the National Water Research Institute were integrated into the present volume.

Lake Ontario is 309 km long and 85 km wide with a mean depth of 85 m. Clearly there are trade-offs between attempting to sample many stations (GLISP) where the ship travels 1200 km to 94 stations or a few representative stations in more detail (LONAS). In LONAS, five stations were sampled on 10 cruises along a transect south from near Port Hope, Ontario (Fig. 1, and Simons and Schertzer 1987), but two were sampled more intensely. One was a nearshore station along the north shore where upwelling is common (401). The other, midlake station 403, is typical of 70% of the lake area. Data obtained from this transect were compared with those from a similar transect studied in 1972 during the International Field Year on the Great Lakes (IFYGL).

The combined effect of surface heating and wind results in stratification patterns and currents which lead to upwelling or downwelling (Simons and Schertzer 1987). Such information is a prerequisite for understanding processes that distinguish large lakes from the small lakes where most of the research on P–chlorophyll relationships has been conducted.

The date for midlake stratification can occur anytime during June and has a profound effect on the year-to-year variation in summer chlorophyll biomass and species composition. During the period of deep mixing, a highly turbulent condition exists which promotes the growth of diatoms (Gray 1987). Sedimentation is an important sink for carbon fixed by the phytoplankton at this time and is important in maintaining the benthic community (Lean et al. 1987b). The longer the period of mixing, the less P remains for the summer population. Statification occurs as a warm layer of water moves out over the lake (Simons and Schertzer 1987), and at this time, diatoms are unable to maintain themselves and sink from the trophogenic zone. The summer phytoplankton population consists of much smaller cells including phototrophic picoplankton which are only about 1 μm in diameter and represent up to 40% of the summer biomass and productivity (Pick and Caron 1987). During summer, sedimentation of P and organic C is much less and nutrients are effectively recycled within the top 20 m through zooplankton grazing (Lean et al. 1987b).

Based on records from 1965 to 1985, the date for stratification was predicted by Rodgers (1987) using the temperature of the lake at its deepest point on 1 April. The 1 April temperature was a function of the mean December–March temperature at Toronto's Pearson International Airport. As Rodgers (1987) points out, 1972 and 1982 were the two most atypical years in the last 20, as stratification did not occur until the end of June. Associated with the El Niño anomaly in the Pacific Ocean, 1983 had the earliest stratification on record.

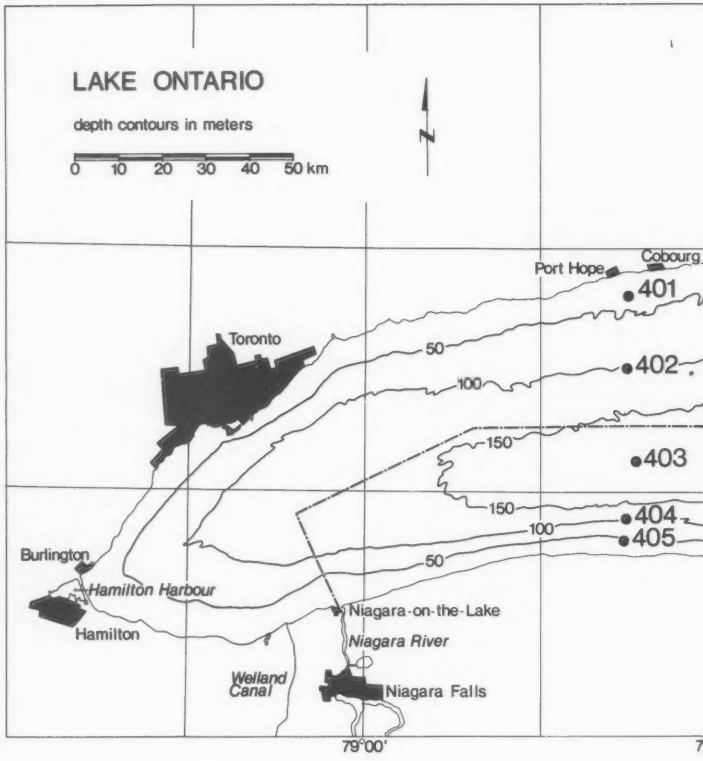
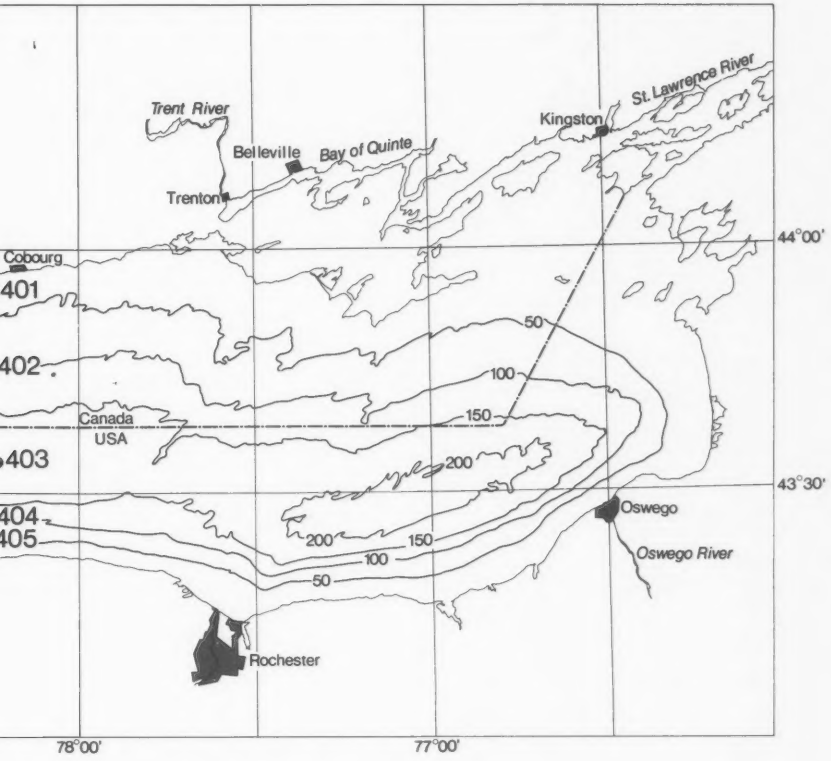


FIG. 1. Bathimetric map of Lake Ontario showing stations



; stations 401, 402, 403, 404, and 405 used in the LONAS investigation.

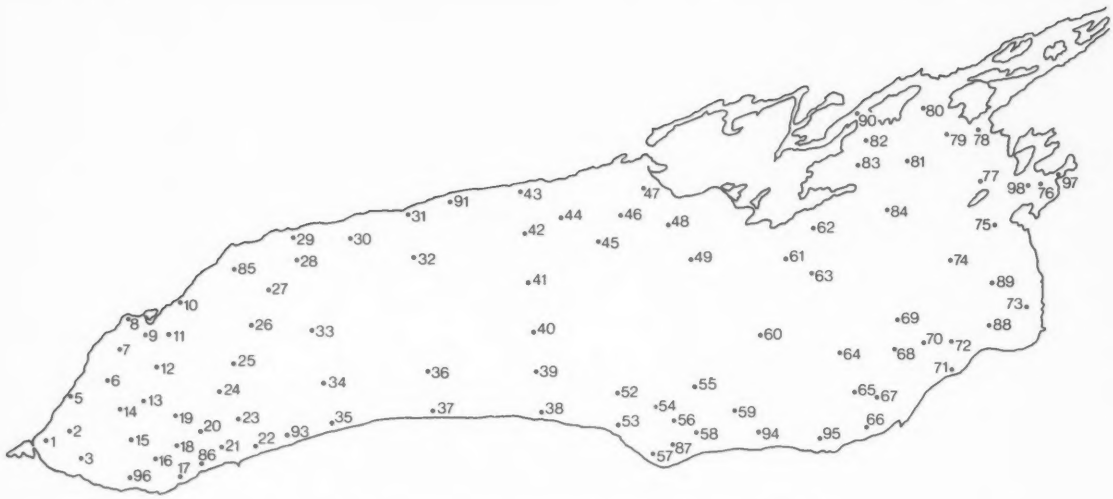


FIG. 2. Lake Ontario stations used for the Great Lakes Surveillance Plan.

Stevens and Neilson (1987) discuss the changes in P loading and remedial action using data from 1968 to the present time. They show that spring soluble reactive phosphate (SRP) has dropped by 70% and spring total phosphorus (TP) is presently half the concentration found in the early 1970's. However, no reduction in summer TP or chlorophyll *a* has been observed. This suggests that spring sedimentation rates were greater during years of peak P loading. Hypothetically, only diatom production from April to July would have been affected by P reductions (Lean et al. 1987b). This may also explain the complete depletion of soluble reactive silica (SRS) and the July metalimnetic chlorophyll peaks observed in 1972 compared with 1982.

The sediment adsorption capacity for phosphate was investigated by Manning (1987). Using Mossbauer spectral and chemical extraction methods, he calculated that sediments bind almost half the current P loadings. This corresponds well with the 60% retention coefficient calculated by Stevens and Neilson (1987).

In contrast with spring TP, spring nitrate concentrations have increased from 230 to 375 $\mu g\ N \cdot L^{-1}$ from 1968 to 1982 (Stevens and Neilson 1987). Denitrification (the conversion of nitrate to nitrous oxide and dinitrogen) can be a sink for excess nitrate but is insignificant in the water column of Lake Ontario due to the high dissolved oxygen concentrations (Lean and Knowles 1987). Minimum summer nitrate concentrations in 1972 were below detection, but now exceed 125 $\mu g\ N \cdot L^{-1}$. Indeed, peak summer chlorophyll biomass was probably N limited in 1972, so without P control the chlorophyll concentrations would now be much higher. It would seem that Lake Ontario has shifted from N limitation to P limitation. It could also be argued that a portion of the nitrate increase was due to P reduction. The N:P ratio in the plankton is about 13, so a reduced use of 10 $\mu g\ P \cdot L^{-1}$ by either the plankton or the littoral community would cause nitrate concentrations to increase by the observed 130 $\mu g\ N \cdot L^{-1}$. However, since the increase in nitrate began before P loading reached its maximum and the rate of increase has changed little since the early 1960's (Stevens and Neilson 1987), the increase in nitrate must be due to increased N loading.

Neilson and Stevens (1987) analyzed 19 variables at 94 stations (Fig. 2) from 21 cruises between March and December 1981 and 1982. During summer stratification, SRP, nitrate, and SRS concentrations declined, but in the surface waters, ammonium and TP increased. An increase in epilimnetic summer TP is not commonly observed in lakes. The distinguishing feature of P loading in Lake Ontario is that it continues through the year compared with most lakes where P loading usually occurs with the spring freshet. While most of the P loading to Lake Ontario is through the Niagara River, this cannot explain the elevated epilimnetic concentrations because the TP concentration in the Niagara River is lower than in Lake Ontario and in effect actually serves to dilute the lake.

Water quality concerns of the 1960's in Lake Ontario did not stem from high chlorophyll *a* concentrations in the midlake. Instead, the public disliked the foul-smelling alga (*Cladophora*,) that washed up and rotted along the shoreline. Painter and Kamaitis (1987) found that the biomass and growth rate of *Cladophora* in 1982 were less than half those in 1972 and developed a model to predict growth rates based on tissue P concentrations. Because much of the growth is due to local inputs, further reductions of P will have even more beneficial effects.

Lean et al. (1987a) and Pick (1987a, 1987b) used physiological indicators (phosphate turnover time, a phosphate deficiency index, photosynthetic depression with nutrient enrichment, alkaline phosphatase activity, carbohydrate to protein ratios) to show that the plankton at the nearshore stations become P deficient in April soon after the thermal bar forms whereas the plankton from the midlake regions do not become P deficient until stratification. Upwelling events in summer reduce the degree of P deficiency as does entrainment of deeper water in fall. New insights into the P status of the plankton were provided by measurements of the subcellular distribution of recently assimilated radioactive phosphate at ambient and enriched concentrations (Lean and Cuhel 1987). Because

incorporation of P will favor polyphosphate storage in P-deficient populations, incorporation patterns can be used to indicate P status.

Net biomass production of plankton populations is a crucial term in models of community dynamics from which phosphate requirements are estimated. Cuhel and Lean (1987a, 1987b) augment the classical methods for primary production measurements to provide detailed information on rates of microplankton biomass production. They measured the rate of incorporation of ^{14}C-labeled bicarbonate and ^{35}S-labeled sulfate into subcellular fractions. Protein synthesis provides a maximum measure of growth. Night protein synthesis by phytoplankton continued at the expense of polymeric carbohydrate and low molecular weight carbon compounds. The 24-h protein synthesis integrated over depth provided doubling times of 10–20 d instead of 3–10 d for total C fixed. The increase in biomass is offset by losses due to zooplankton grazing and sedimentation. During the summer, P was effectively recycled through community excretion processes and sedimentation losses were low. During the deep mixing period prior to summer stratification, sedimentation of the diatom community was the principal pathway for P and C losses (Lean et al. 1987b).

Fixation of ^{14}C-labeled bicarbonate during bottle incubations was susceptible to photoinhibition to near-surface irradiances. Putt et al. (1987), using DCMU-enhanced fluorescence, demonstrated that this was usually a bottle artifact caused by incubating samples at fixed depths. In the lake, phytoplankton circulation must occur on a time scale of hours, thus preventing photochemical damage from affecting photosynthesis of unconstrained populations in situ. By not including photoinhibition in the productivity calculation, values were 30% higher.

While N is no longer the limiting nutrient, the recyling processes are rapid and scientifically interesting. Regeneration of ammonium through community excretion caused a summer increase in ammonium. Nitrification by chemoautotrophic bacteria was principally responsible for ammonium uptake and consequent elevation of nitrite levels also in late summer (Lean and Knowles 1987). During summer stratification, nitrate assimilation into microbial biomass (primarily phytoplankton) greatly exceeded its regeneration through nitrification; hence, epilimnetic nitrate concentrations declined throughout the stratified summer season. The entire flux of nitrate-N proceeded initially through microbial particulate organic nitrogen (PON) for which four principal fates can be identified: (1) increase of PON; (2) deaminative regeneration of ammonium for (a) subsequent nitrification to nitrite or (b) assimilation into microbial PON; or (3) sedimentation. These three processes can account for two thirds of the nitrate flux. The remaining one third sets the upper limit for (4) biomass-N of higher organisms in the food web, including fish. This quantity was equivalent to about half of the N demand for protein synthesis calculated by Cuhel and Lean (1987b) and equal to the nitrate assimilation rates calculated using ^{15}N-labeled nitrate. Indeed, these data may provide an upper limit for fish yield.

Most rate measurements are made on operationally defined fractions rather than specific groups which make up the aquatic community. At best, one can only quantify flux rates between different size classes rather than specific groups or trophic levels. The fraction of living to nonliving for each size class is unknown. Zimmermann et al. (1987), using differential thermal analysis and thermal gravimetric analysis, characterized the particulate material in the water column and sediments. They showed that a high proportion of the particulate fraction was detritus. This complicates studies on rate measurements. For example, diurnal changes in ^{14}C-labeled subcellular biopolymers were observed (Cuhel and Lean 1987b) but a large fraction of detrital material would obscure net changes measured chemically. Furthermore, if most of the particulate C is detritus, generation times are underestimated.

Roughly half of the particulate C can be accounted for by microscopic examination, but despite problems in interpretation, microscopic enumeration provides information useful in describing the community and can be used to monitor year-to-year changes. Attempts to measure plankton abundance have followed breakthroughs in technology. It was once thought that there were fewer than 10^2 bacteria$\cdot$mL^{-1} using agar plates. Later through the use of improved light microscopy the quantity increased to over $10^4\cdot$mL^{-1}. Using epifluorescence microscopy, Pick and Caron (1987) found that bacteria increased over the season from 1×10^6 to $6 \times 10^6\cdot$mL^{-1}. Furthermore, up to 10^5 bacteria$\cdot$mL^{-1} contained chlorophyll and accounted for up to 40% of the autotrophic biomass and productivity. In previous investigations the latter organisms would simply be called "bacteria" or missed entirely. Leppard et al. (1987) characterized the picocyanobacteria using electron microscopy.

Flagellates have been previously recognized as a significant component of the Lake Ontario plankton, but Pick and Caron (1987) showed that roughly half of these 2- to 10-μm organisms contain no photosynthetic pigment and live heterotrophically. This changes the classical picture of community structure with phytoplankton as primary producers being eaten by zooplankton. Concepts of trophodynamics must be altered to recognize that some of the bacteria are capable of photosynthesis, while some "algae" derive their metabolic needs by eating bacteria. Growth rates of summer heterotrophic bacteria may be as high as three doublings per day but are kept in check by grazing, principally by heterotrophic flagellates.

Too often when a new technique is discovered, traditional methods are discontinued. Without long-term data, changes in ecosystems cannot be assessed. While it is now recognized that the Utermöhl method for algal enumeration cannot be used to quantify very small (0.2–2 μm) organisms, it has been the method used up to the present time. Consequently, Gray's (1987) measurements are particularly important because they permit comparisons with previous investigations. Since 1972, major changes in algal community composition were not observed.

Historical zooplankton data were of little use for comparison with the present study, since net diameters, mesh sizes, depth of vertical haul, and methods of preservation were not consistently followed over the years. Nevertheless, when Taylor et al. (1987) compared their data with those from 1970, there was little change in the time of appearance or abundance of dominant species, suggesting that recent stocking of salmonid fishes has not yet restructured the Lake Ontario food web.

Traditionally, zooplankton enumeration neglected the smaller (<64 μm) forms. Falling between the size of organism seen with the eyes of the compound microscope used for algal enumeration and the binocular microscope used for major zooplankton enumeration are the ciliated Protozoa. Taylor and Heynen (1987) describe the seasonal and depth distribution for these organisms. Lake surveys rarely included these organisms, yet in our case they represent up to 15% of the zooplankton biomass. Because of their high metabolic rates, they and the rotifers probably account for much of the grazing, especially before the appearance of the Cladocera in August.

Our original objective was to determine the duration and degree of P limitation in Lake Ontario throughout the season. This was accomplished and new insights into the flux of nutrients and energy were established. For example, all the ambient P was taken up and replaced in minutes during the summer period, zooplankton consume the equivalent of the entire nanoplankton biomass every 10 d, and regeneration of nutrients is in balance with growth requirements during the summer season. Changes in TP concentrations have been significant in the last 10 yr, but changes in community structure and biomass have been difficult to document. Epifluorescent microscopy has opened our eyes to the most metabolically active part of the Lake Ontario ecosystem, with autotrophic picoplankton responsible for a significant portion of the primary productivity and heterotrophic flagellates consuming the entire heterotrophic bacteria community in less than a day.

While it is well known that organisms can bioconcentrate contaminants in the absence of food intake, bioenergetic models are useful in predicting the fate of heavy metals in fish and organic contaminants in birds. The processing of material through the food web must be understood more completely if we are to anticipate the impact of man's activities on our aquatic ecosystems.

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Stratification, Currents, and Upwelling in Lake Ontario, Summer 1982

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A description is presented of physical measurements carried out on Lake Ontario during the summer of 1982. Seasonal variations of stratification and circulation are illustrated by monthly averages of temperature and current distributions in a north–south cross section of the lake. Day-to-day variations of temperature and currents are presented for three periods coinciding with biochemical investigations along the same transect of the lake. A wind-induced upwelling event followed by alongshore propagation of a warmwater wave is described and the dynamics involved are discussed.

Des mesures physiques faites sur le Lac Ontario au cours de l'été 1982 sont présentées. Les variations saisonnières de la stratification et de la circulation sont illustrées par des moyennes mensuelles de températures et par la distribution des courants dans une coupe transversale nord–sud du lac. Les variations quotidiennes de la température et des courants sont présentées pour trois périodes coïncidant avec des recherches biochimiques effectuées le long de la même coupe transversale du lac. Une remontée d'eau profonde due au vent, suivie par la propagation le long de la rive d'une vague d'eau chaude, est décrite, et la dynamique du phénomène est analysée.

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Coinciding with the Lake Ontario Nutrient Assessment Study (LONAS), extensive physical measurements were carried out on Lake Ontario during a 4-mo period from early May to late August 1982. Continuous time series of temperatures, currents, and winds were obtained from eight fixed-temperature profilers, 40 self-recording current meters, four meteorological buoys on the lake, and a number of shore-based meteorological stations. Most of the instruments were located in the LONAS cross section of Lake Ontario between Port Hope, Ontario, and Point Breeze, New York. Two coastal transects were established 30 km east and west of the main transect. The location of the transects and the network of meteorological stations are shown in the upper part of Fig. 1. The depth profile of the central section is shown in the lower part of Fig. 1 with current meters identified by black circles and fixed-temperature profilers by solid vertical lines.

The purpose of this paper is to provide a description of the stratification cycle and circulation patterns encountered in Lake Ontario during the spring and summer of 1982. In addition, detailed analyses of temperatures and currents will be presented for three periods coinciding with ship cruises along the LONAS transect. The periods are June 28 – July 2, August 9–13, and August 23–27. Large day-to-day variations in currents as well as temperature will be shown to occur in the course of each cruise. In view of the pronounced spatial variations of temperatures and nutrients in large lakes, the currents transport different water masses into the measurement area which must be anticipated to have a significant impact on biochemical processes in these lakes.

Seasonal Stratification and Circulation

The seasonal stratification cycle of a lake results from the combined effects of surface heating and wind. In early spring the water is colder than the temperature at maximum density (4°C), and hence, surface heating leads to complete mixing of the vertical water column until the temperature approaches 4°C. In the shallow shore zones this warming is rapidly accomplished and followed by stratification with a "thermal bar" separating these zones from the fully mixed open lake. As the statification spreads out over the whole lake, the intensity of wind-induced turbulence determines the level to which the surface heat is mixed down, and hence, the thermocline in the open lake tends to deepen during stormy periods. In the shore zones, large thermocline displacements are caused by wind-induced surface currents normal to the shore which are compensated by return flow at lower levels and vertical motions at the shore.

The above elements of the seasonal stratification cycle are vividly illustrated in Fig. 2. The top of Fig. 2 shows the eastward component of the wind stress at the surface of Lake Ontario obtained in the usual way from the square of the measured wind. It is known from Ekman's work in the early 1900's that, due to the earth's rotation (Coriolis effect), the wind-driven surface transport tends to be to the right of the wind. Therefore, the eastward component of the wind stress is primarily responsible for upwelling along the north shore and downwelling along the south shore. The bottom of Fig. 2 shows the behavior of the 10° isotherm measured by the fixed-temperature profilers at the north shore, midlake, and south

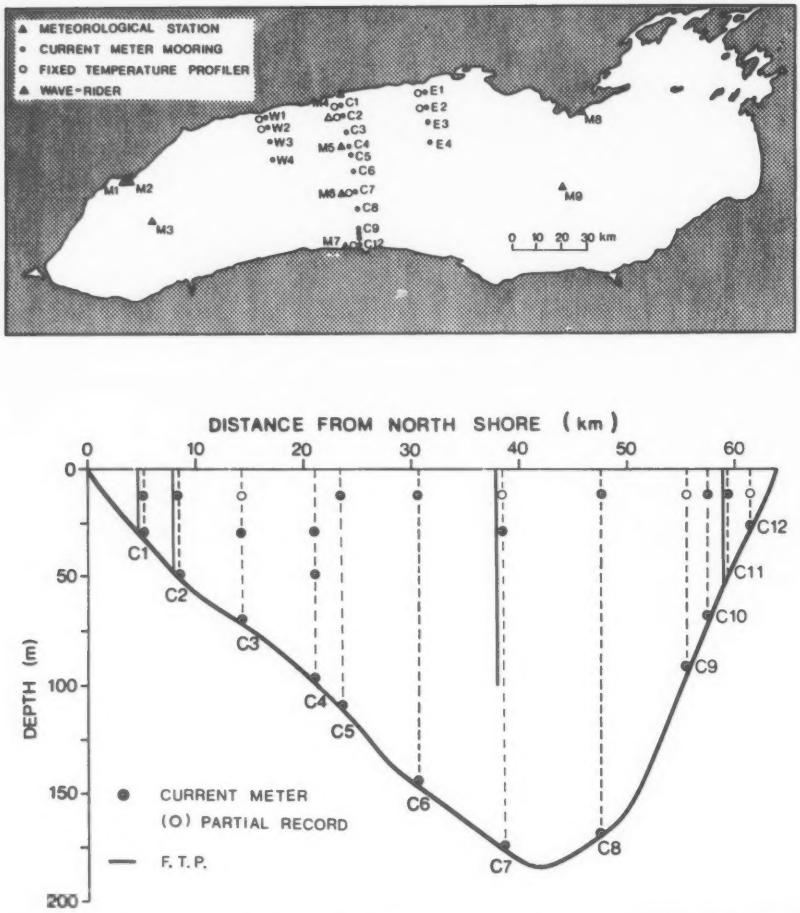

FIG. 1. Location of current meters, fixed-temperature profilers (F.T.P.), and meteorological stations in Lake Ontario, summer 1982.

shore, respectively. It is apparent that the deepwater stratification lags the nearshore stratification by more than a month and, once established, the thermocline depth in midlake remains more or less at the same level. At opposing shores, the thermoclines move in opposite directions and are clearly forced by the wind. An eastward wind causes southward surface drift and hence upwelling at the north shore and downwelling at the south shore; a westward wind has the opposite effect.

A suitable display of temperature and current variations may be obtained by interpolating all available observations in the LONAS cross section of Lake Ontario. As shown in the lower part of Fig. 1, temperature observations for this transect are available from four fixed-temperature profilers, each providing continuous records at 20 depths. In addition, continuous time series of temperature are available from 24 current meters in this cross section. These observations were interpolated by the following procedure. First, vertical temperature profiles were constructed at the location of each current meter mooring by adopting the shape of the profile measured by an adjacent temperature profiler and shifting this profile up or down to match the temperatures measured by the current meters. A total of 10 vertical temperature profiles was thus obtained for the cross section. Next, temperatures were interpolated horizontally between temperature profiles at vertical intervals of 1 m between the surface and 30 m.

Monthly averaged temperatures obtained by this procedure are presented in the upper half of Fig. 3. The temperature distribution in May was clearly dominated by the thermal bar at the shallow north shore. The thermal bar at the much deeper south shore did not develop until the end of May. In June, the stratification in the shore zones increased gradually but the open lake remained colder than 4°C and hence continued to be fully mixed between the surface and the bottom. In July, the stratification in this section of the lake was fully established with the thermocline sloping upward toward the north shore and downward toward the south shore. This was partly a remnant of the thermal bar episode and partly the result of generally eastward winds (see top of Fig. 2) which, as noted earlier, tend to cause a drift of warm surface waters to the south. During August the average temperature distribution remained nearly

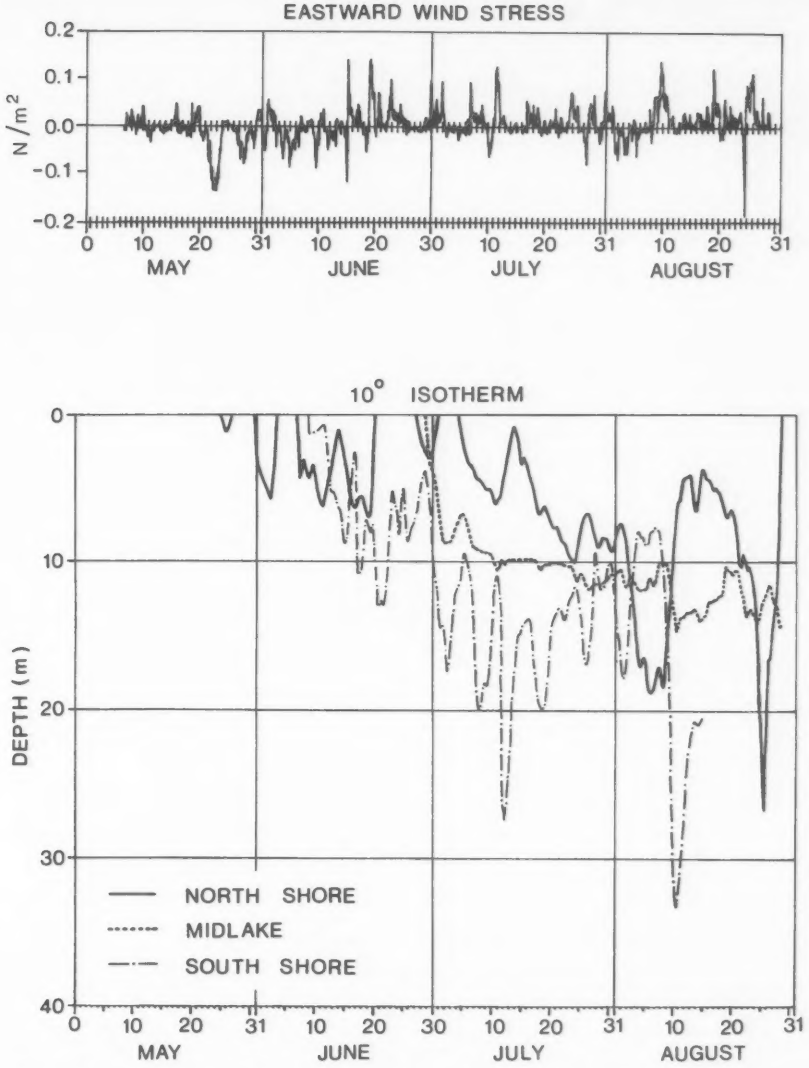

FIG. 2. Eastward component of wind stress and depth of 10° isotherm in Lake Ontario, summer 1982.

the same, but it will be seen in the following that strong day-to-day variations were induced by wind events.

The currents were interpolated in the same manner as the temperatures. Although no continuous vertical profiles of currents were measured, they may be inferred from the temperature profiles. In the absence of stratification, currents are vertically uniform and the same holds true below the thermocline during the stratified season. Between the thermocline and the surface, vertical variations of currents may also be expected to be relatively small, and hence, the major shearing currents are concentrated around the thermocline. Thus, when the thermocline depth exceeds 10 m, the upper current meter provides an estimate of the epilimnion current, while the bottom current meter measures the hypolimnion current. The transition from upper to lower layer current may be taken to match the temperature profile. Once the vertical current profile has been established for each mooring, horizontal interpolation is readily accomplished.

The lower half of Fig. 3 shows monthly averages of the component of the current normal to the LONAS transect. The units are kilometres per day; positive values represent eastward currents and negative currents run westward. The total flow of water through a cross section of a closed lake must vanish when averaged over periods of a few days or longer. For Lake Ontario the total transport should be equal to the average flow from the Niagara to the St. Lawrence River. If the results of Fig. 3 are averaged over the whole period of the experiment, the total transport is 10^4 m^3/s to the east, which compares favorably with the Niagara discharge of 7×10^3 m^3/s. Similar eastward transports are found for the months of June and August. However, the net transport for July is two to three times as large, while the net transport during May is westward. Fortunately,

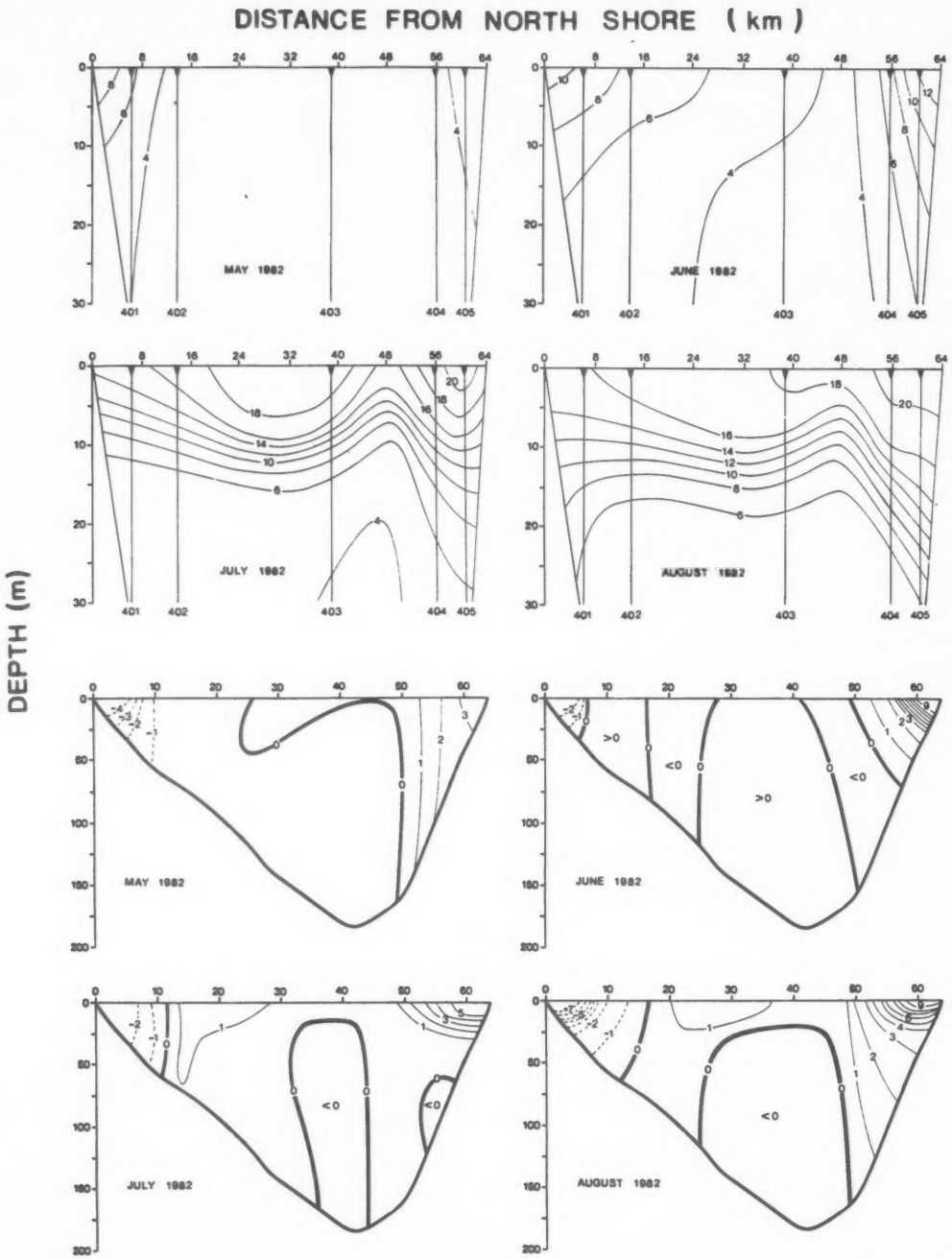

FIG. 3. Monthly averaged distributions of temperature (above) and currents (below) in the cross section of Lake Ontario between Port Hope, Ontario, and Point Breeze, New York. Vertical lines in temperature graphs identify the five LONAS stations 401–405.

these errors can be most likely attributed to inaccuracies in the deep lake currents which are too small to be accurately observed but make significant contributions to the total water transport because of the large water depths.

The most interesting aspects of Fig. 3 are the persistent boundary currents near the two shores. Along the south shore the water flows from west to east with surface velocities of 5–10 km/d. On the north shore the water flows from east to west. The boundary currents can be traced back to the thermal bar episode which is known to be associated with counterclockwise circula-

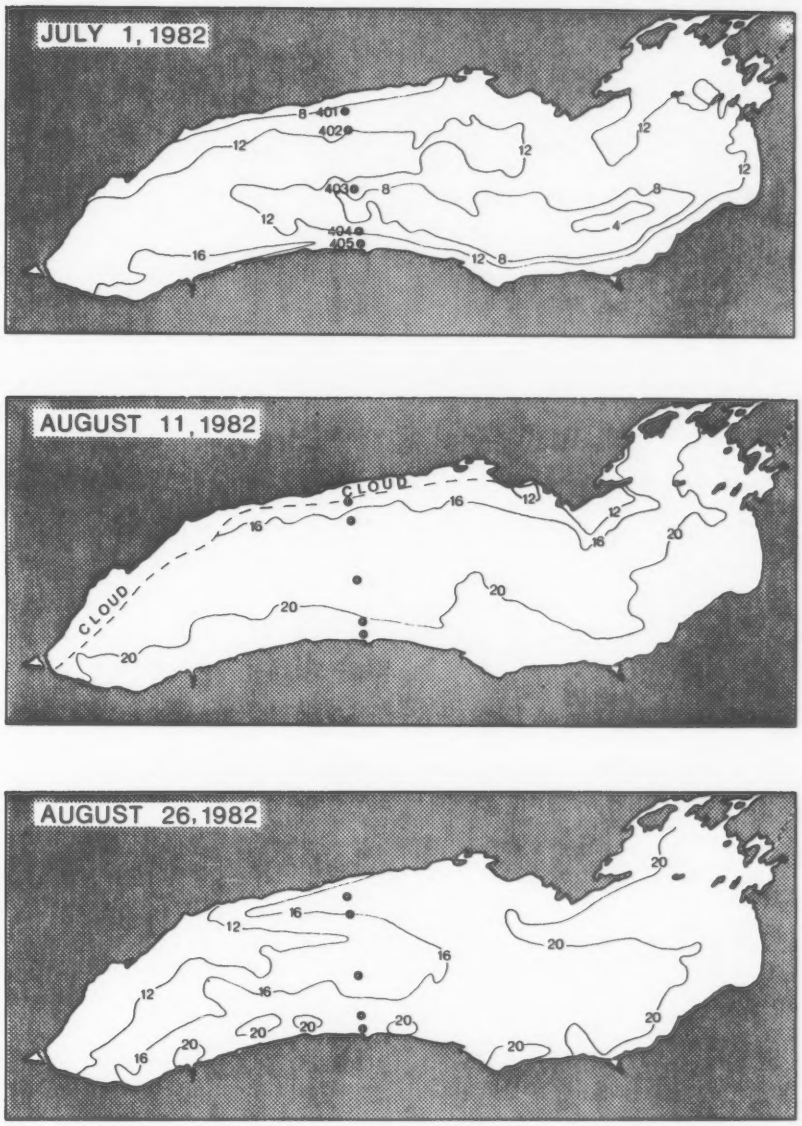

FIG. 4. Satellite observations of surface water temperatures in Lake Ontario. Black circles show the five LONAS stations.

tion around the perimeter of the lake. Although affected by a few summer storms, the currents appear to persist throughout the season.

Short-Term Variations of Temperature and Currents

Detailed descriptions of temperature and currents will be presented for three periods coinciding with biochemical cruises: June 29 – July 2, August 10–13, and August 24–27. The overall temperature distributions in Lake Ontario during these periods are illustrated in Fig. 4. During the first period, the deep-lake station was just getting stratified and winds from westerly directions resulted in upwelling of cold water at the north shore. The second period was dominated by 3 d of strong winds from the west, again causing upwelling along the whole north shore. By the time of the third period, the cold northshore water had drifted into the western basin due to dynamical processes discussed later in this paper.

Day-to-day variations of temperature and currents for each period are shown in Fig. 5-7. The upper part of each figure presents temperature distributions for the LONAS cross section. These results were obtained by the same procedure used for the monthly averages of Fig. 3. The lower part of each figure shows daily averaged currents through the LONAS cross section. To

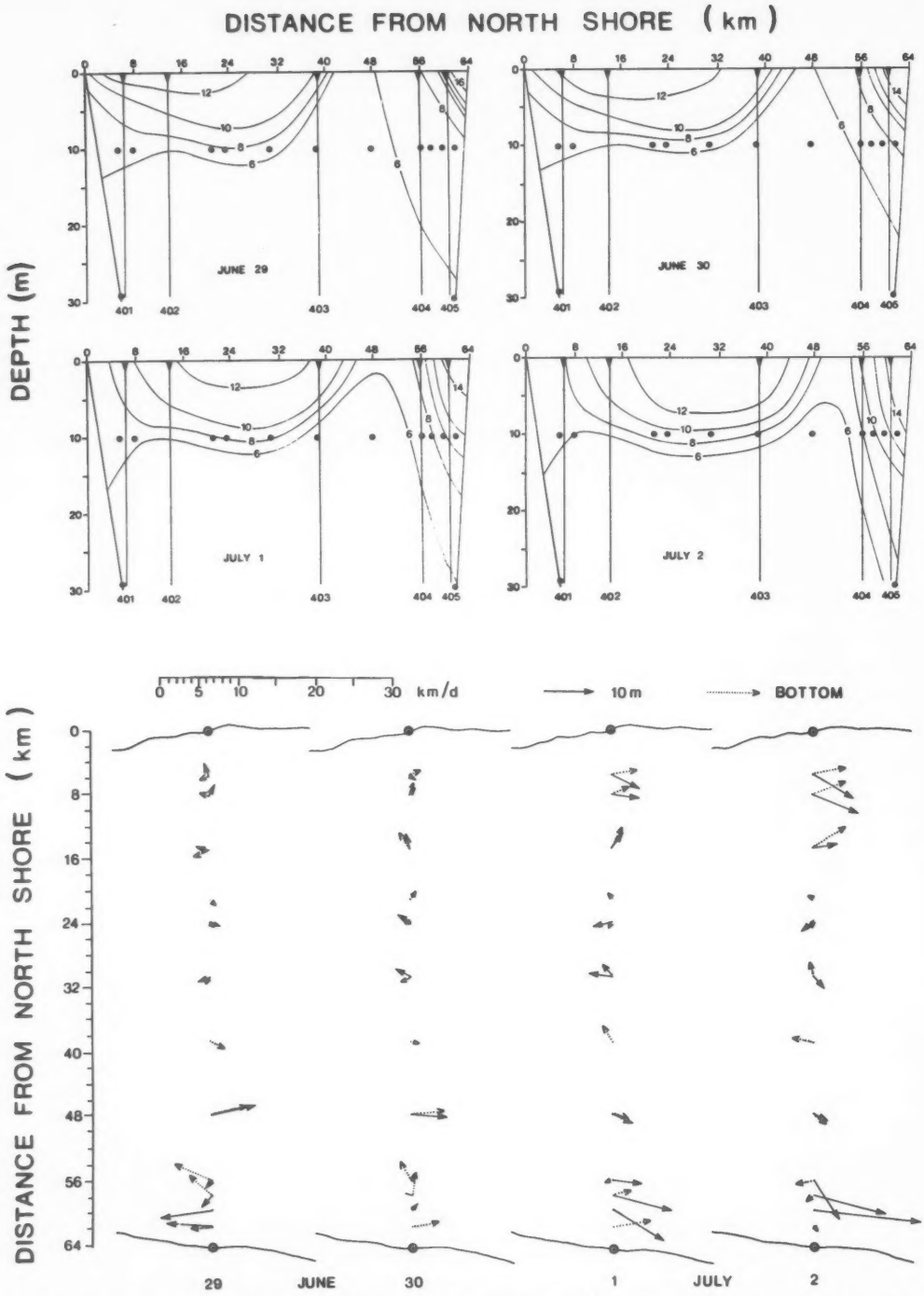

FIG. 5. Daily temperatures (above) and currents (below) in the Lake Ontario cross section between Port Hope, Ontario, and Point Breeze, New York, June 29 – July 2, 1982. Vertical lines in temperature graphs identify the LONAS stations. Black circles in current graphs show locations of Port Hope and Point Breeze.

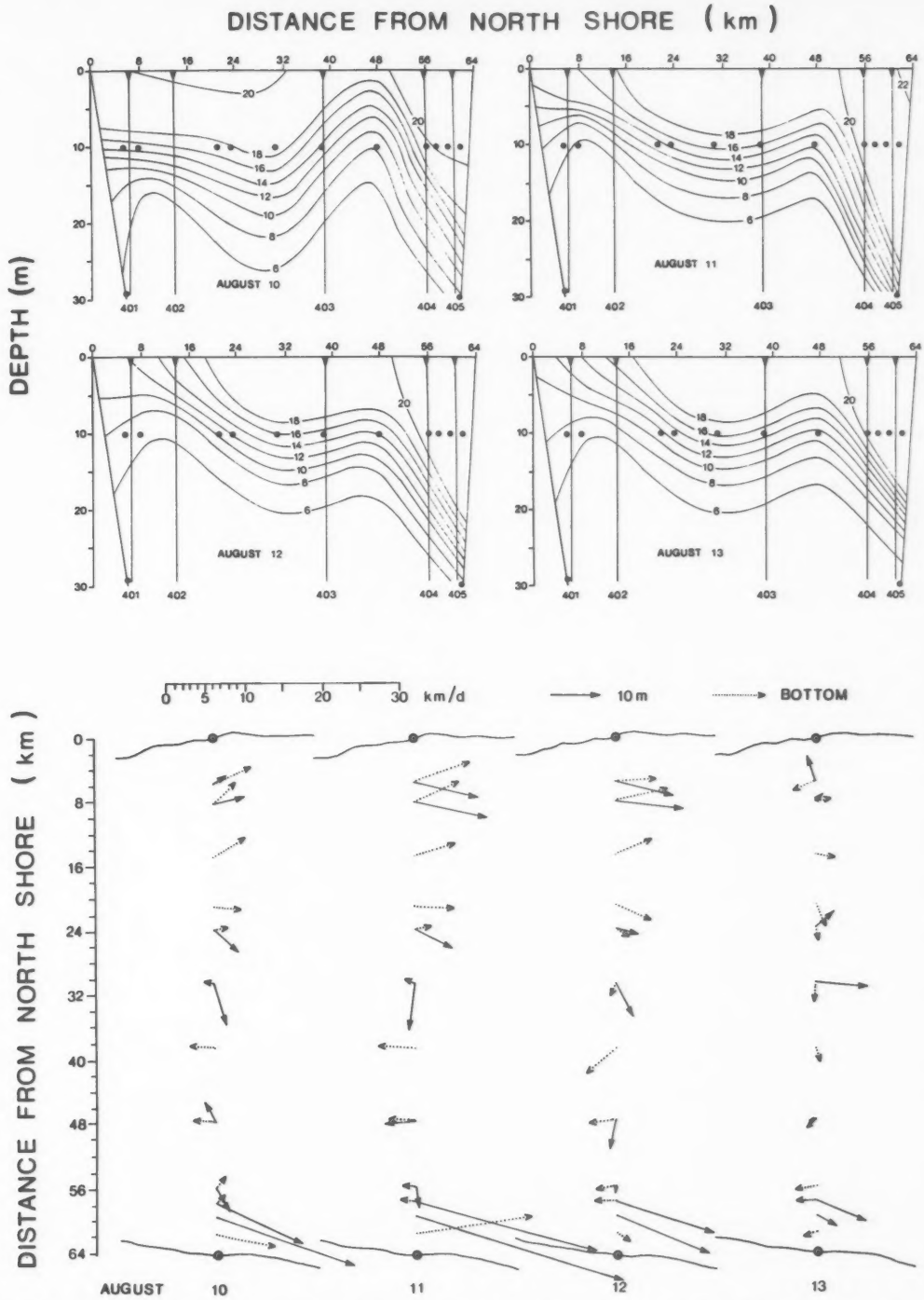

FIG. 6. Daily temperatures (above) and currents (below) in the Lake Ontario cross section between Port Hope, Ontario, and Point Breeze, New York, August 10–13, 1982.

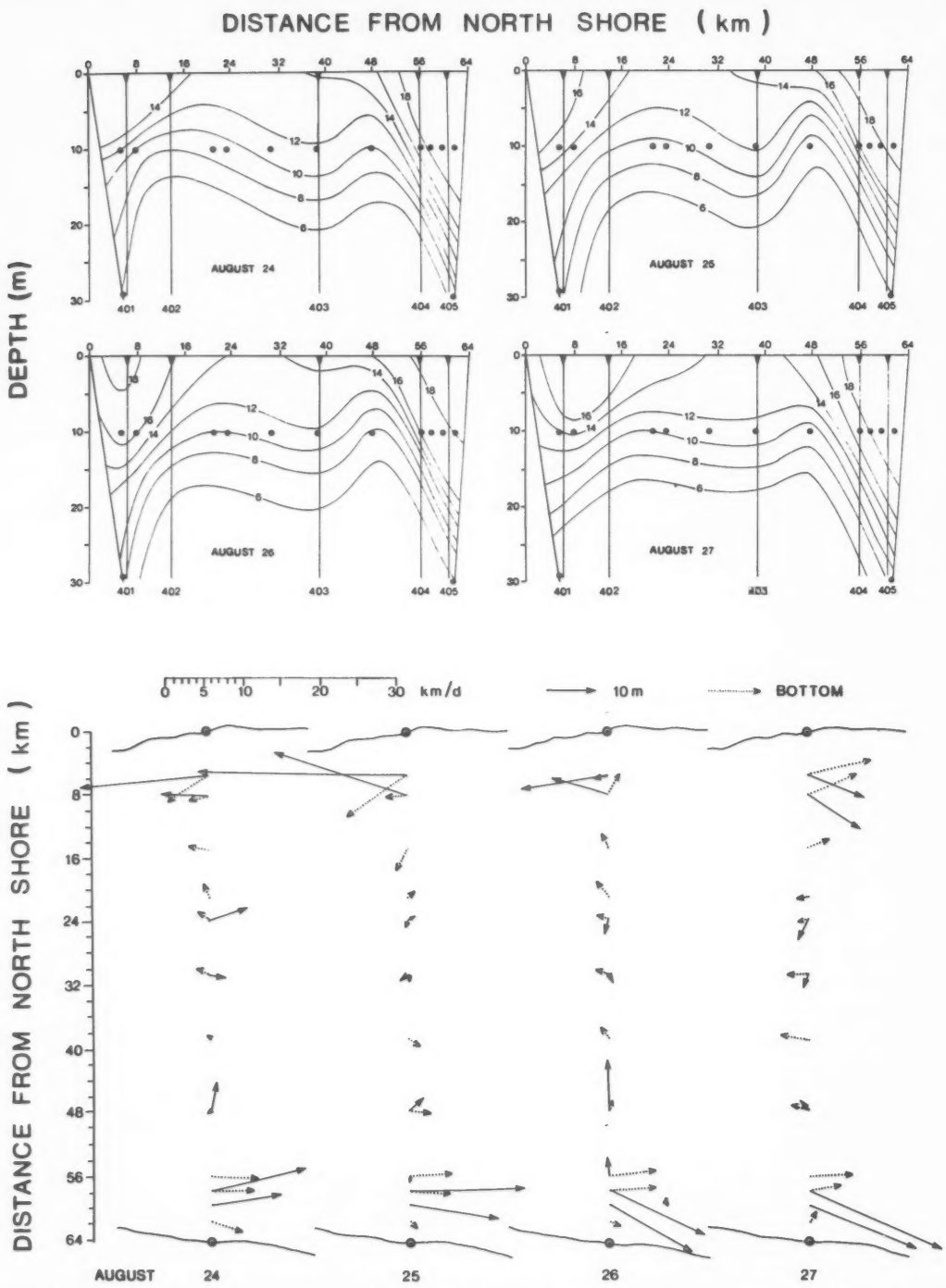

FIG. 7. Daily temperatures (above) and currents (below) in the Lake Ontario cross section between Port Hope, Ontario, and Point Breeze, New York, August 24–27, 1982.

facilitate comparison with the temperature distributions, the current meter positions are shown by black circles in the temperature maps.

In the course of the first period, an eastward wind started blowing over the lake (see top of Fig. 2). The initial effect of such a wind is to move water to the east end of the lake such that the surface will slope down against the wind. The subsequent currents result from the counteracting effects of wind and surface slope. The surface slope creates a pressure gradient which is not affected by the depth of a water column. However, the wind stress is much more effective in moving shallow water than deep water. Since, as noted earlier, the total transport through a cross section of a closed lake must vanish, the net result of these opposing forces is that the shallow nearshore water moves in the direction of the wind, while the midlake water returns against the wind. This explains the generation of eastward currents along both shores (Fig. 5). Near the north shore the currents were weaker and more uniform than at the south shore. The reason is that the northshore stratification was weakened by upwelling, and hence, the wind forcing could be mixed down to accelerate the whole water column. By contrast, the southshore water was strongly stratified and the wind moved only the relatively thin upper layer. In addition, the surface currents are seen to be more southward than the bottom currents. This agrees with the aforementioned Ekman theory which predicts surface drift to the right of the wind resulting in upwelling at the north shore and downwelling at the south shore.

During the second episode the wind blew again to the east, and hence, the lake reacted in the same way as before. However, in this case the wind stopped in the middle of the 4-d period, and consequently, the thermocline started returning to its original position. This was particularly noticeable on the south shore. Near the north shore a broad band of eastward currents was observed on August 11 but the speeds decreased rapidly after the storm and the currents reversed themselves 2 d later. At the south shore, strong eastward currents were generated which again were confined to the wedge of warm water. At the peak of the storm the thermocline was depressed below the level of the bottom current meter in the mooring adjacent to the south shore. This explains the large dotted arrows pointing to the east in that location.

The final episode was affected by two wind events, a short but strong westward wind impulse on August 25 followed by eastward winds on August 26. At first glance this sequence of events might seem to explain the initial downwelling and westward flow along the north shore and the subsequent upwelling and current reversal. However, it will be shown presently that these events were caused primarily by the passage of a warmwater wave. Indeed, near the south shore the wind seemed to have little effect and a strong eastward current persisted throughout this episode.

To investigate the northshore temperature and current variations in more detail, use was made of observations in the coastal transects 30 km east and west of the main transect (Fig. 1). Alongshore distributions of temperature were obtained by the same interpolation procedure used for the cross-sectional distributions. Figure 8 presents daily alongshore temperature patterns at a distance of 5 km from the north shore for August 20–27. The vertical line in the centre of each figure represents the intersection with the LONAS cross section; the left side coincides with the coastal transect to the west and the right side with the transect to the east. Daily values of observed currents are shown by arrows. The results show a wave of warm water progressing from east to west along the north shore and being accompanied by strong westward surface currents. The dynamics involved in this event will be discussed below.

Dynamics of Coastal Upwelling

The theory of wind-induced upwelling in large lakes contains two basic elements. The first element concerns the forcing of coastal upwelling by local winds. According to Ekman theory, the wind causes a 10- to 20-m-deep surface layer to move to the right of the wind due to the Coriolis force of the earth's rotation. Therefore, an alongshore wind tends to generate a surface current normal to the coast. In order to maintain a mass balance in the coastal zone, the surface drift must be offset by a return current at lower levels and the two are joined together by vertical motion at the coast. Thus, a wind blowing along the shore with the land on the left causes upwelling and a wind blowing in opposite direction causes downwelling. It has been shown by Charney (1955) that, in presence of stratification, thermocline displacements due to upwelling or downwelling decrease rapidly with offshore distance such that coastal upwelling or downwelling affects only a strip of a few kilometres adjacent to the shore.

The second element of the theory of coastal upwelling deals with the way a pattern of upwelling and downwelling, once established by the wind, propagates around the lake. From the foregoing it follows that a uniform wind blowing over a lake causes upwelling at the shore to the left of the wind and downwelling at the shore to the right but has little or no effect at the upwind and downwind shores where the alongshore component of the wind vanishes. By unfolding the whole shoreline of the lake into a straight shore, it is easy to visualize that the wind-induced thermocline excursions display a wave-like variation along the shore with wavelength equal to the perimeter of the lake. A thermocline wave of this type which, as noted above, is confined to a narrow strip near the coast is known as an internal Kelvin wave. Such waves move with the speed of gravity waves on the interface between layers of fluid of different density, but due to the Coriolis force of the earth's rotation they remain trapped at the shore and propagate with their right shoulder to the shore (in the Northern Hemisphere); that is, counterclockwise around the Great Lakes. This alongshore propagation of warm and cold water after major upwelling events was first observed in Lake Michigan by Mortimer (1963), and a theoretical discussion for idealized lakes was presented by Csanady (1968). This Kelvin-wave mechanism is responsible for the wave propagation seen in Fig. 8.

From the foregoing it follows that upwelling at a given location depends not only on local wind forcing but also on the history of wind-induced upwelling at other points around the lake because these disturbances may eventually propagate into the region of interest. On this basis, a workable theory of wind-induced upwelling in large lakes was developed in the early 1970's by Bennett (1973), Bennett and Lindstrom (1977), Csanady and Scott (1974), Gill and Clarke (1974), and Clarke (1977). This theory will now be used to explain observed thermocline movements at the north shore of Lake Ontario after the storm of August 9–11, 1982.

The first step is to compute the alongshore component of the wind stress at regular intervals around the shore, since it is this component which drives the upwelling or downwelling. Given the wind, the alongshore component for each shoreline interval follows from the local orientation of the shoreline relative to the

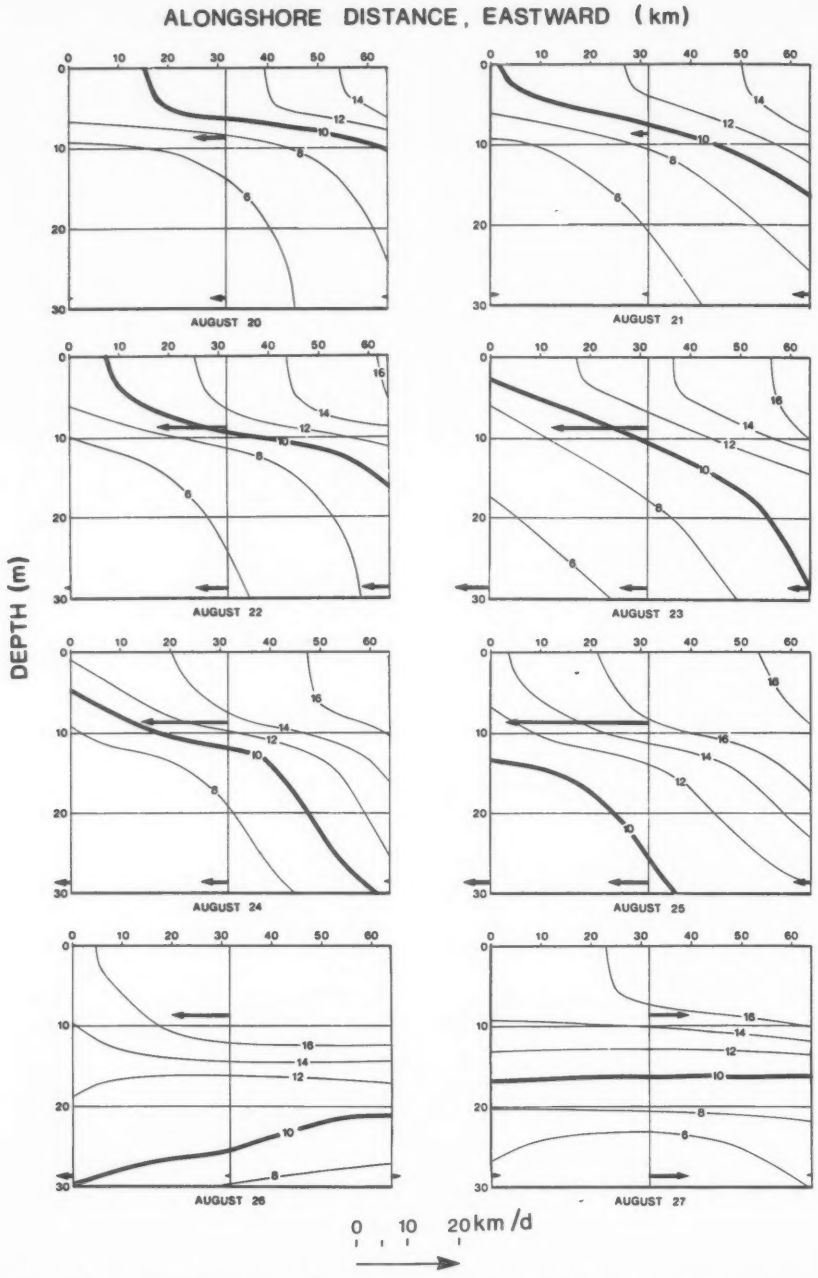

FIG. 8. Daily values of alongshore temperature variations 5 km off the north shore of Lake Ontario, August 20–27, 1982.

wind direction. By way of illustration, the mean wind stress for the August 9–11 storm is shown by the arrow at the centre of Lake Ontario in Fig. 9 and a few alongshore stress components are shown by arrows at selected shore locations. The actual calculations were carried out at 5-km intervals along the shore. The middle of Fig. 9 shows the same information after the shoreline has been unfolded into a straight line, starting from the west end of the lake and proceeding in a clockwise direction around the perimeter. Note that the arrows along the south shore now point to the left because the shore lies to the right of the local wind direction. The bottom of Fig. 9 presents the resulting thermocline excursions at the shore measured relative to the

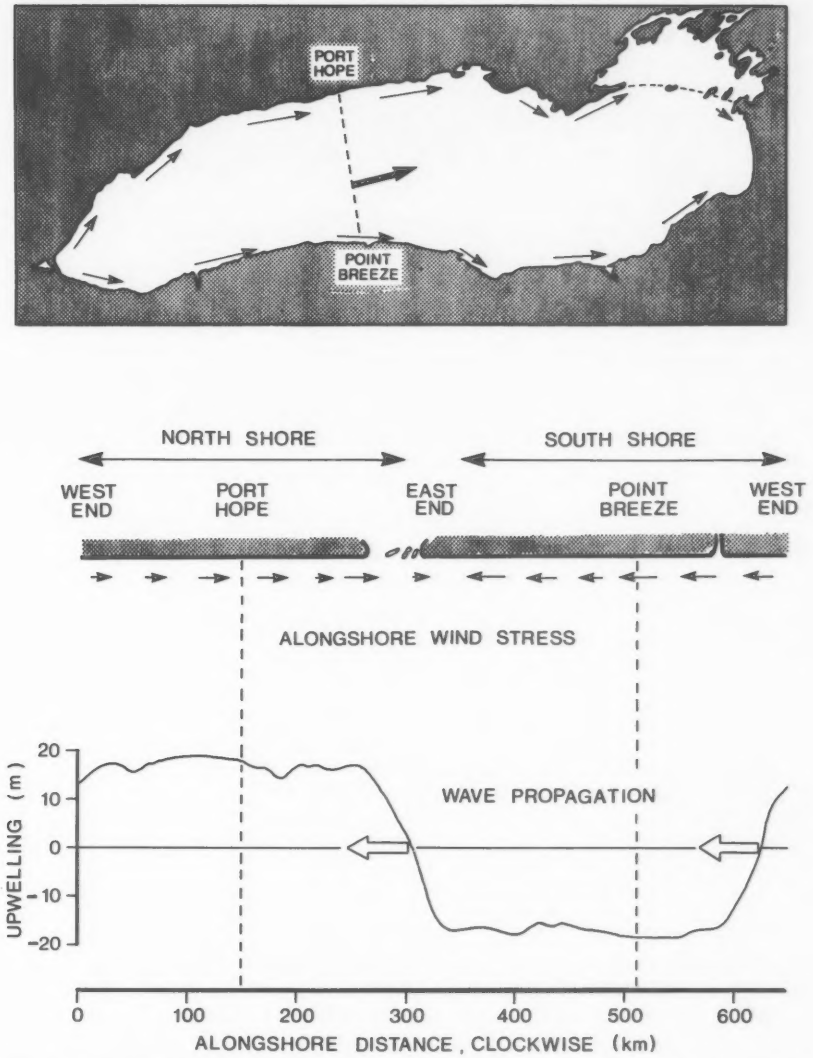

FIG. 9. Alongshore component of wind stress during storm of August 9–11, 1982, and resulting thermocline excursions computed from a simple upwelling model.

thermocline level before the storm. These excursions are proportional to the alongshore stress component integrated over the duration of the storm. According to theory, the proportionality factor is $C/(\epsilon gh)$ where C is the internal wave speed, ϵ is the density difference across the thermocline, g is the earth's gravity, and h is the mean thermocline depth. Based on Fig. 2, estimated values are $\epsilon = 0.0015$ and $h = 12$ m, while the empirical model of Bennett and Lindstrom (1977) for Lake Ontario suggests that $C = 20$ km/d. The average stress for the 3-d storm period is 0.054 N/m^2, and thus the theoretical thermocline excursion during the storm is 18.3 m. This compares favorably with the observations in Port Hope and Point Breeze (Fig. 2).

The next step of the calculation is to move the thermocline wave along the shoreline such that the shore is to the right of the direction of propagation. Thus the wave moves to the left in Fig. 9 as indicated by the open arrows. With the above propagation speed of 20 km/d, the wave front would reach Port Hope by August 19, a little earlier than indicated by the observations of Fig. 8. However, a number of additional effects will modify the shape of the wave as it propagates along the shore. In the first place, allowance must be made for a gradual damping of wave amplitude due to bottom and shoreline irregularities and mixing across the thermocline. Secondly, although the storm of August 9–11 accounts for most of the subsequent thermocline movements, each of the following wind events makes a similar, but smaller, contribution. Therefore, the above procedure must be repeated for each wind event and the results must be added. Since effects of past winds are gradually damped out, the result at any given time depends primarily on the more recent wind

events. Finally, as shown by Bennett (1973), nonlinear effects cause the warmwater wave to steepen into a warm front.

To conclude this discussion, a few words may be added regarding the currents associated with wind-induced thermocline movements. According to the above upwelling model, the thermocline excursions are accompanied by alongshore currents in a narrow coastal strip. Above the thermocline the currents run with the shore on their left in upwelling zones and with the shore on their right in downwelling areas. Thus the surface water flows in the same direction as the wind arrows shown in Fig. 9. As the wave moves to the left, so does the current pattern. Thus the eastward currents induced by the wind on the north shore will turn to the west as the warm water approaches. The current meter observations of Fig. 8 show the expected strong westward surface currents following the passage of the warm front.

Acknowledgements

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Response of Lake Ontario to Reductions in Phosphorus Load, 1967–82

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Stevens, R. J. J., and M. A. Neilson. 1987. Response of Lake Ontario to reductions in phosphorus load, 1967–82. Can. J. Fish. Aquat. Sci. 44: 2059–2068.

Total phosphorus (TP) loading to Lake Ontario has declined from 14 600 $t \cdot yr^{-1}$ in 1969 to 8900 $t \cdot yr^{-1}$ in 1982. Midlake spring TP has responded rapidly to these reductions, decreasing at the rate of 1.09 $\mu g \cdot L^{-1} \cdot yr^{-1}$ from a maximum of 30.6 $\mu g \cdot L^{-1}$ in 1973 to 12.8 $\mu g \cdot L^{-1}$ in 1982. Spring soluble reactive phosphorus (SRP) exhibited a proportionally larger decrease than TP such that 1982 SRP was 33% of 1973 levels, compared with 42% for TP. A multiple regression equation indicated an 80% response time of spring TP within 2 yr and a 90% response time within 4 yr. Spring nitrate plus nitrite has increased since 1969 at the rate of 9.5 $\mu g \cdot L^{-1} \cdot yr^{-1}$ causing N:P ratios to increase from 10 to 32. Mean summer epilimnetic TP declined at the rate of only 0.3 $\mu g \cdot L^{-1} \cdot yr^{-1}$ from 1977 to 1982 so that mean summer TP levels now exceed spring TP by 1–2 $\mu g \cdot L^{-1}$. This suggests that loading to the lake during the stratified period has not shown a similar decline and may be responsible for the lack of a trend in algal biomass indicators during this period.

Dans le lac Ontario, la charge de phosphore total (PT) est passée de 14 600 $t \cdot a^{-1}$ en 1969 à 8 900 $t \cdot a^{-1}$ en 1982. La teneur en PT printanier au milieu du lac a réagi rapidement à ces diminutions : à raison de l,09 $\mu g \cdot L^{-1} \cdot a^{-1}$ elle est passée d'un maximum de 30,6 $\mu g \cdot L^{-1}$ en 1973 a 12,8 $\mu g \cdot L^{-1}$ en 1982. Le phosphore réactif soluble (PRS) printanier a montré une plus importante baisse proportionnelle que le PT de sorte que le PRS en 1982 ne s'élevait qu'à 33 % du niveau observé en 1973, contre 42 % dans le cas du PT. Une régression multiple a révélé un temps de réaction de 80 % du PT printanier en moins de 2 ans et un temps de réaction de 90 % en moins de 4 ans. Depuis 1969, le nitrate et le nitrite printaniers ont monté à raison de 9,5 $\mu g \cdot L^{-1} \cdot a^{-1}$, ce qui s'est traduit par une augmentation des rapports N:P de 10 à 32. Dans l'épilimnion, le PT moyen en été a baissé à raison de 0,3 $\mu g \cdot L^{-1} \cdot a^{-1}$ de 1977 à 1982 de sorte que les niveaux moyens de PT estival dépassent maintenant les niveaux printaniers de 1–2 $\mu g \cdot L^{-1}$. Ceci porte à croire que la charge pendant la période de stratification n'a pas montré une baisse semblable, ce qui peut expliquer l'absence d'une tendance chez les indicateurs de la biomasse algale pendant cette période.

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Prior to 1964, few comprehensive water quality studies had been carried out on Lake Ontario that would permit an accurate assessment of its trophic state. The first comprehensive study, completed in 1916, was concerned principally with bacterial levels from raw sewage discharges (International Joint Commission 1918). Further studies were carried out from 1946 to 1948, and while the growing problem of industrial pollution was acknowledged, levels of bacteria and dissolved solids received the focus of attention (International Joint Commission 1950).

Despite the lack of supporting data, studies began to appear in the literature attesting to the increasing eutrophication of Lake Ontario. Schenk and Thompson (1965) reported a doubling of the mean annual biomass of phytoplankton at the Toronto water intake from 1923 to 1954, with a shift in dominant genera similar to that of Lake Erie. Beeton (1969) cited an increase in total dissolved solids (140–200 $mg \cdot L^{-1}$) from 1910 to 1965, coupled with the collapse of the lake herring (*Coregonus artedii*), lake trout (*Salvelinus namaycush*), and blue pike (*Stizostedion vitreum glaucum*) fisheries during 1955–65, as evidence of the degradation of Lake Ontario water quality. Unfortunately, these studies relied on data collected from localized and possibly nonrepresentative areas.

In 1964, amidst growing concern over the continuing decline of water quality in Lake Ontario, the governments of Canada and the United States directed the International Joint Commission to study and report on the occurrence, sources, extent, and causes of transboundary pollution and recommend remedial measures. To oversee the implementation of field studies necessary to achieve this purpose, the International Lake Ontario – St. Lawrence River Water Pollution Board (ILOWPB) was formed.

Surveys carried out during the period 1964–68, under the auspices of the ILOWPB, were comprehensive in geographic scope and, for the first time, included nutrient (P and N) variables. It was concluded from these studies that, while morphometrically oligotrophic, Lake Ontario had water quality characteristic of mesotrophic lakes, with specific areas (Hamilton Harbour, Bay of Quinte, Toronto Harbour) being eutrophic (ILOWPB 1969). The ILOWPB attributed 57% of the total phosphorus (TP) load to municipal and industrial inputs and 33% to inputs from Lake Erie. Further, they estimated that detergent phosphates contributed 70% of the entire TP load (ILOWPB 1969). Using Vollenweider's (1968) loading plot, it was determined that the admissible and dangerous loading limits for Lake Ontario were 0.4 and 0.8 $g \cdot m^{-2} \cdot yr^{-1}$, respec-

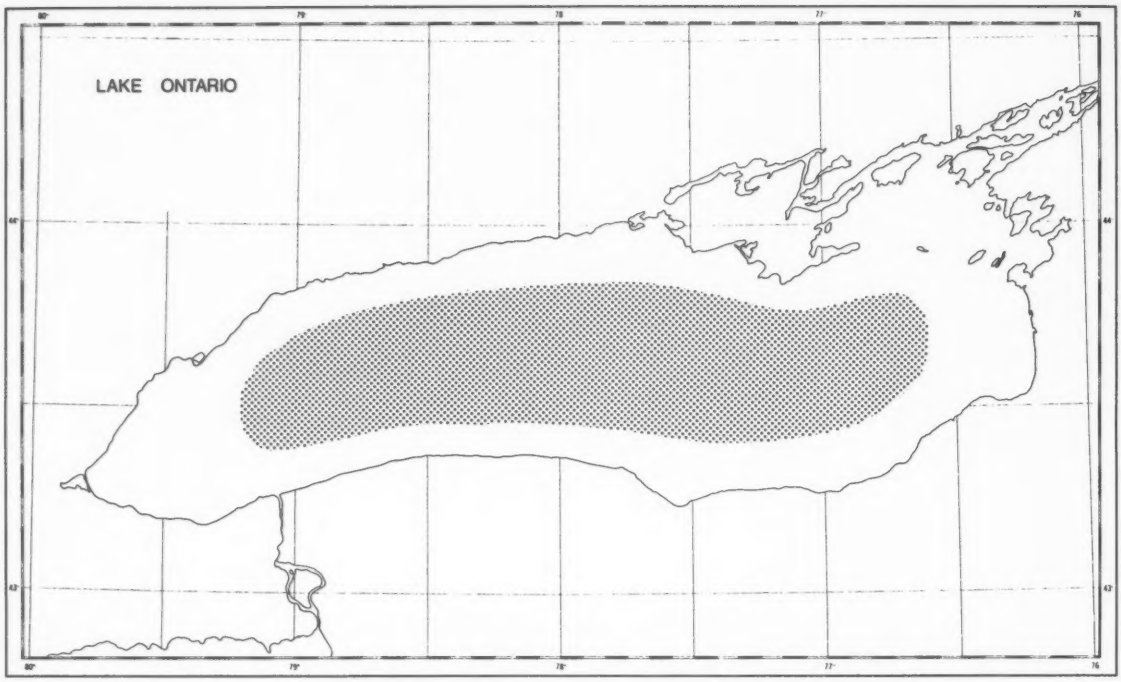

FIG. 1. Midlake region (shaded) of Lake Ontario selected for trend analysis.

tively. Current (1968) load was estimated to be 0.7 $g \cdot m^{-2} \cdot yr^{-1}$, and the projected load for 1986, based on population and industrial growth estimates, would be 1.4 $g \cdot m^{-2} \cdot yr^{-1}$ in the absence of ameliorative measures. Consequently, it was recommended that phosphates in detergents be replaced with an environmentally acceptable substitute and that municipal treatment plants be required to achieve a further 80% reduction in P levels after the removal of detergent P (ILOWPB 1969).

To satisfy these recommendations, the government of Canada enacted legislation, effective August 1, 1970, that limited the phosphate content of detergent, as P_2O_5 to 20%. This limit was further reduced to 5% by December 31, 1972. The states of New York and Indiana followed suit, imposing a limit of 20% in 1972 and 1.1% in 1973 (Municipal Abatement Task Force 1983). More significant was the signing of the Great Lakes Water Quality Agreement in 1972. In this document, the programs necessary to control P were outlined including specifications for construction and operation of municipal waste treatment plants and upgrading of those plants discharging in excess of one million gallons per day to attain P effluent concentrations of 1.0 $mg \cdot L^{-1}$.

In the following years, numerous and more complex models were developed, some based on Vollenweider's (1968) original steady-state, input–output model (Dillon and Rigler 1974a; Vollenweider 1976; Chapra 1977; Vollenweider and Kerekes 1980), and others based on dynamic mass balance principles, incorporating allowances for phytoplankton and zooplankton interaction (Thomann et al. 1976). Based on this new information, it was concluded that to achieve an average TP concentration of 10 $\mu g \cdot L^{-1}$ in Lake Ontario, an estimated load of 6800 $t \cdot yr^{-1}$, or 0.36 $g \cdot m^{-2} \cdot yr^{-1}$ must be achieved (Task Group III 1978). This recommendation was incorporated into the 1978 Great Lakes Water Quality Agreement and a P target load of 7000 $t \cdot yr^{-1}$ was established.

One requirement common to both the 1972 and 1978 agreements was that surveillance and monitoring programs be continued to assess the extent of eutrophication and the effect of reduced P loading. Since 1975, the Water Quality Branch of Environment Canada has maintained a monitoring program in the offshore waters of Lake Ontario. Two objectives of this program were to provide statistically reliable water quality trend information and to relate changes in water quality to remedial measures. This paper summarizes nutrient and biomass data collected from 1968 to 1982 in the context of these two objectives.

Methods

Eighty-one lakewide surveys were carried out at approximately monthly intervals on Lake Ontario from 1968 to 1974, with station density and location varying considerably between cruises. An additional 73 surveys were completed from 1975 to 1982 utilizing the station pattern described in Neilson and Stevens (1987). Specific details related to station locations, cruise frequency and duration, and analyses and measurements carried out are available in Kwiatkowski and Neilson (1983) and methods of chemical analyses are given in detail in the *Analytical Methods Manual* (Environment Canada 1979).

Only midlake stations encompassed in the shaded area in Fig. 1 were employed in the statistical analysis of data, as they were not subject to localized inputs or thermal bar effects. This resulted in a minimum of 8 and a maximum of 14 stations being included in the analysis for the 1968–73 period and 25 stations

for the 1974–82 period. To ensure that results from stations within this area were meaningful in a whole-lake context, their mean values for TP, particulate organic carbon (POC), particulate organic nitrogen (PON), and chlorophyll *a* corrected (Chl *a*) for each cruise were compared with their respective whole-lake, area-weighted mean values. In each case, the results from the midlake region were significantly ($p < 0.001$) correlated with the whole-lake mean.

In determining long-term trends (1968–82) in nutrient variables (TP, soluble reactive phosphorus (SRP), nitrate plus nitrite ($NO_3 + NO_2$), total filtered nitrogen (TFN)), only data collected from the 1 m sampling depth during vernal turnover (March–April) were used, as this represents the period between winter regeneration and the onset of spring growth. Furthermore, samples collected at 1 m have been shown to be representative of the entire water column at this time (Neilson and Stevens 1987). Trend determinations were based on cruise mean values, as variability associated with station pattern was assumed to be random. Heteroscedasticity (i.e. cruise variance proportional to cruise mean) was significant ($p < 0.05$) only for TP and SRP, and consequently, these data were log-transformed to approximate normal distributions prior to being subjected to trend determination.

Trends in algal biomass indicators (POC, PON, Chl *a*) were investigated only for the period 1974–82, as sampling and analytical methods used prior to this were incompatible with the more recent data. Before attempting to detect trends, data were partitioned on the basis of seasons, as we did not expect to find any relationship between algal biomass and P during the spring. A stepwise multiple linear regression analysis relating the biomass indicators (POC, PON, Chl *a*) to mean surface temperature (MST) and TP was used to investigate this. We first restricted our analysis to cruises where MST < 15°C, as Lean et al. (1983) have demonstrated that, in Lake Erie, P rapidly becomes strongly limiting to phytoplankton once thermal stratification is completely established. Examination of vertical temperature profiles for Lake Ontario revealed that complete thermal stratification coincided with a midlake MST of 15°C. We repeated this analysis for those cruises in the fall where MST < 15°C, as increasing SRP concentrations at this time (Neilson and Stevens 1987) again suggested nonlimiting conditions.

Trend analysis of algal biomass indicators during the stratified period (MST > 15°C) was restricted to the results of only 23 cruises between 1974 and 1982. Within-year ranges in biomass indicators were large, with maximum ranges of 2.23, 226.6, and 40.2 $\mu g \cdot L^{-1}$ for Chl *a*, POC, and PON, respectively, and would likely obscure any real trend. To reduce this variability, a statistical relationship between the algal biomass indicators and two independent variables, julian day (JD) and MST, was established, thus serving to remove seasonal effects from the data (Rutherford 1984). Using MST as an independent variable in a Model I regression violates one of the assumptions of the regression model, i.e. that the independent variable be measured without error. However, as the variability associated with MST was extremely small during the summer period (coefficient of variability ~ 5%), this violation was not considered severe.

To examine the relationship between algal biomass and spring TP, the deseasonalized data were regressed against time. In contrast, when attempting to establish a relationship between algal biomass and summer TP for those cruises where both were measured (1976–82 exc1uding 1980), we looked for a direct relationship between the deseasonalized biomass indicators and summer TP, since the overall trend in mean summer TP was considerably less than that of spring TP.

Phosphorus load estimates for municipal and industrial point sources, monitored tributaries (with adjustments for unmonitored tributaries), and atmospheric contributions for 1967–76 were calculated by Fraser (1979). Those for 1977–82 are as reported annually by the Surveillance Work Group to the Water Quality Board of the International Joint Commission. As both sets of estimates were determined by similar methods, we assumed that effects of error or bias on data interpretation were minimal.

Results

Phosphorus and Nitrogen

Ambient concentrations of spring TP responded rapidly to changes in load (Fig. 2). During the period 1969–73, TP exhibited a highly significant ($p < 0.001$) increasing trend with time at the rate of 1.05 $\mu g \cdot L^{-1} \cdot yr^{-1}$. Subsequent to 1973, however, a highly significant ($p < 0.001$) decreasing trend was observed at the rate of 1.09 $\mu g \cdot L^{-1} \cdot yr^{-1}$. Log-transformed SRP responded rapidly to changes in TP, exhibiting a highly significant ($p < 0.001$) correlation with TP from 1969 to 1982 (Fig. 3). More importantly, SRP decreased at a proportionally greater rate than did TP such that 1982 SRP was 33% of 1973 concentrations, compared with 42% for TP.

Mean summer epilimnetic TP has not exhibited the same decreasing trend as spring TP. With the exception of 1976, when levels averaged 23.1 $\mu g \cdot L^{-1}$, summer TP has exhibited only a slight reduction, decreasing from 16.7 in 1969 to 14.4 $\mu g \cdot L^{-1}$ in 1982. In fact, since 1977, mean summer TP has decreased at the rate of only 0.3 $\mu g \cdot L^{-1} \cdot yr^{-1}$, despite a decrease of 1.6 $\mu g \cdot L^{-1} \cdot yr^{-1}$ in spring TP over the same period. The result of these contrasting trends is that mean epilimnetic summer TP now exceeds spring TP by 1–2 $\mu g \cdot L^{-1}$ whereas in 1969 and 1972, mean summer TP was approximately 5–7 $\mu g \cdot L^{-1}$ less than spring TP levels.

$NO_3 + NO_2$ has exhibited a dramatic rise since 1969, increasing at the rate of 9.5 $\mu g \cdot L^{-1} \cdot yr^{-1}$ which is equivalent to an increase of 15.5×10^3 $t \cdot yr^{-1}$ (Fig. 4). In contrast, dissolved organic nitrogen (DON), calculated as TFN minus $NO_3 + NO_2$ and NH_3, has shown no discernible trend from 1972 (when TFN sampling was initiated) to 1982 (Fig. 4). Similar increases in $NO_3 + NO_2$ have been reported for Lake Huron (15.0×10^3 $t \cdot yr^{-1}$, Stevens et al. 1985) and for Lake Superior (42.0×10^3 $t \cdot yr^{-1}$, C. H. Chan, Canada Centre for Inland Waters (CCIW), Burlington, Ont., unpubl. data), suggesting that a common source, such as atmospheric deposition, may be responsible. Further analysis of the relative contributions from other sources, particularly fertilizer applications, is required to verify this.

Due to increases of $NO_3 + NO_2$ coincident with reductions in P, spring N:P ratios increased markedly from 10 in 1973 to 32 in 1982 (Fig. 5). It is only possible to determine TN:TP ratios for 1976–82 when TFN and PON samples were being collected concurrently. However, since DON does not exhibit any seasonal depletion (R. Stevens, CCIW, unpubl. data), suggesting that $NO_3 + NO_2$ and NH_3 represent that fraction of TN available for algal utilization, we computed spring N:P ratios as $(NO_3 + NO_2 + NH_3)$:TP.

Algal Biomass

All three algal biomass indicators (POC, PON, Chl *a*) in the

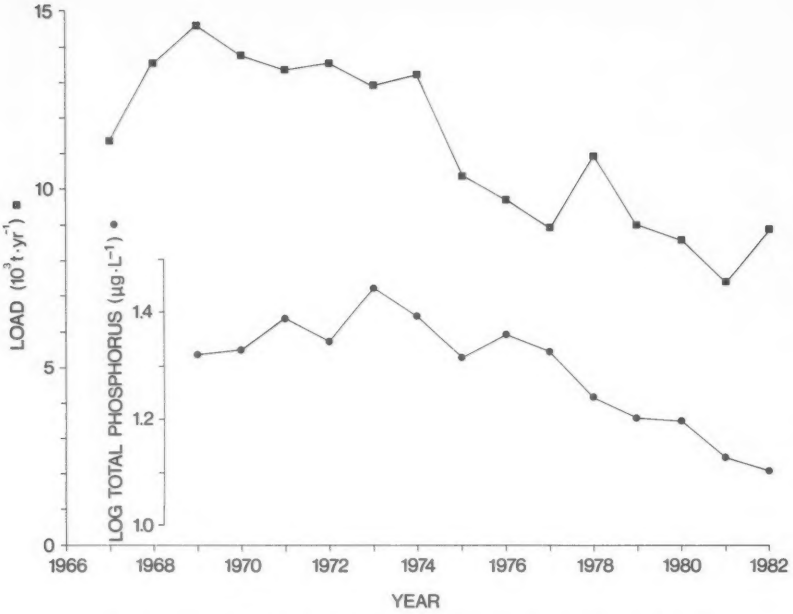

FIG. 2. Annual TP load and spring TP concentrations for the period 1967–82.

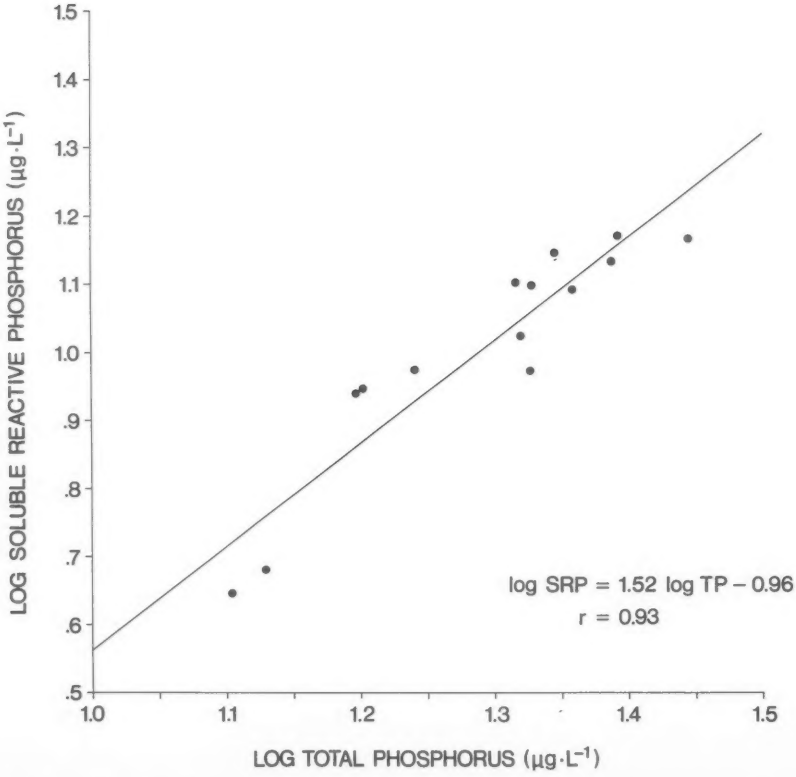

FIG. 3. Changes in log-transformed spring SRP in relation to changes in log-transformed TP from 1969–82.

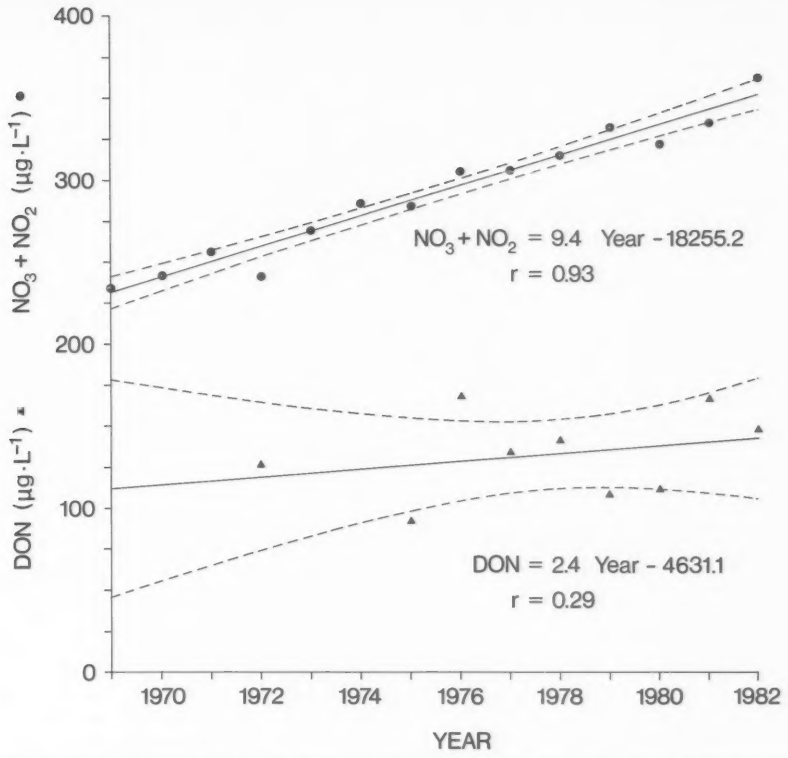

FIG. 4. Trend in spring NO_3 + NO_2 from 1969 to 1982 and DON from 1972 to 1982. Broken lines denote 95% confidence interval of the regression line.

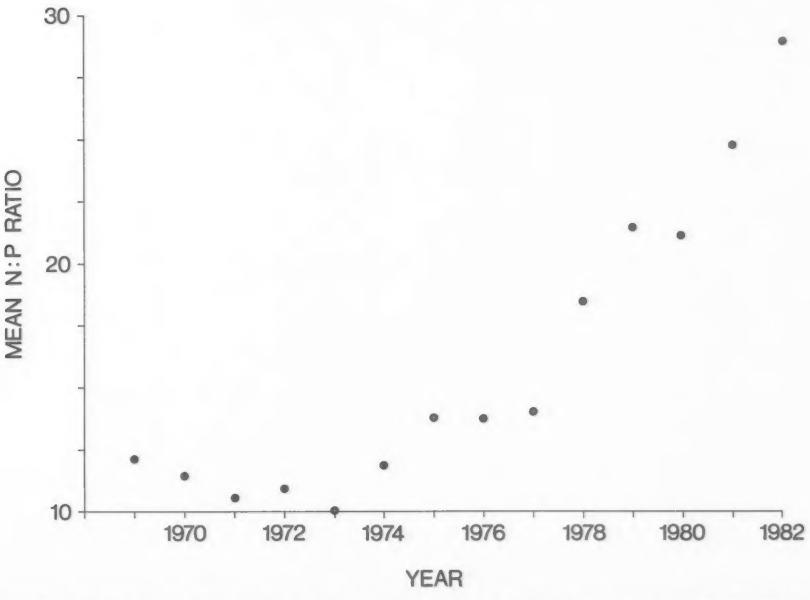

FIG. 5. Change in spring N:P ratio (N calculated as NO_3 + NO_2 + NH_3; P calculated as TP) from 1969 to 1982.

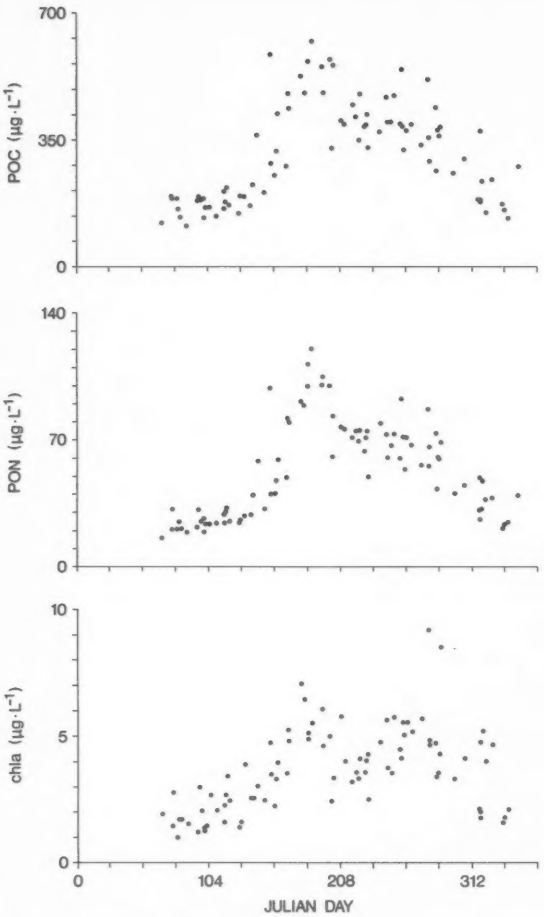

FIG. 6. Seasonal distribution of POC, PON, and Chl *a* combined for the years 1974–82.

offshore waters of Lake Ontario during 1974–82 exhibited bimodal distributions (Fig. 6); consequently, our ability to detect a trend in mean summer algal biomass is strongly dependent on the timing and number of cruises used in deriving the mean, as well as how the stratified period is defined.

Results of the regression analysis between the algal biomass indicators and MST and TP indicated that, during spring, almost 80% of the variability in Chl *a*, and approximately 90% of the variability in POC and PON, is attributable to temperature (Table 1). Repeating this analysis for the fall period provided similar results, with approximately 50% of the variability in Chl *a*, 87% in PON, and 78% in POC being attributable to temperature. Inclusion of TP was significant ($p < 0.05$) only in the spring and fall POC regression analyses, but it accounted for less than 4% of the remaining unexplained variation in POC. It was concluded that algal biomass in the spring and fall is almost entirely a function of temperature and, consequently, light. Therefore, our restriction of trend analysis of algal biomass to those cruises where MST exceeded 15°C was appropriate.

During the stratified period (MST > 15°C), POC and PON showed highly significant ($p < 0.005$) relationships with the

TABLE 1. Determination of dependence of biomass indicators (POC, PON, Chl *a*) on MST and TP by stepwise multiple regression.

Season	Dependent variable	Independent variable entered	Significance	r^2	r^2 change
Spring	POC	Step 1 MST	0.000	0.90	0.90
		Step 2 TP	0.006	0.92	0.02
	PON	Step 1 MST	0.000	0.92	0.92
		Step 2 TP	0.670	0.92	0.00
	Chl *a*	Step 1 MST	0.000	0.79	0.79
		Step 2 TP	0.074	0.81	0.02
Fall	POC	Step 1 MST	0.001	0.78	0.78
		Step 2 TP	0.048	0.82	0.04
	PON	Step 1 MST	0.001	0.87	0.87
		Step 2 TP	0.307	0.87	0.00
	Chl *a*	Step 1 MST	0.042	0.50	0.50
		Step 2 TP	0.426	0.51	0.01

independent variable as (JD − 235), where JD represents the actual sampling date and 235 is the JD at which the minimum of the bimodal curve occurred. The JD representing the minimum of the curve was selected simply by substituting all JD's falling in the summer period (200–265) into the independent expression and selecting for the best fit ($r = 0.58$ and 0.80 for POC and PON, respectively). In contrast with POC and PON, Chl *a* exhibited a more significant relationship with temperature ($p < 0.005$, $r = 0.70$) than with JD. Long-term trends in biomass indicators, therefore, were evaluated using two different methods.

Ranges of the deseasonalized data were reduced considerably when seasonal effects were removed (Chl *a*, 29%; POC, 18%; PON, 41%). Nevertheless, no significant ($p < 0.05$) decreasing trend in time associated with decreasing spring TP concentrations was observed, nor was any found between the deseasonalized algal biomass data and summer TP.

Response to Remedial Measures

We attempted to relate ambient spring TP to annual load using a multiple regression model. By adjusting the time lag between the loading year and spring TP, and selecting for the optimum goodness of fit, we determined the best descriptor of spring TP concentrations to be

$$\log \mathrm{TP} = 22.4A_{(t-2)} + 12.1A_{(t-3)} + 17.5A_{(t-4)} + 0.676$$

where A = load $(\times 10^{-6})\cdot \mathrm{yr}^{-1}$ and t = year, where $t - 2$ represents a lagtime of 2 yr.

This analysis indicated that 80% of the change in spring TP could be accounted for by the load of 2 yr previous and 90% when the third and fourth years previous were included. Surprisingly, the load of the year immediately preceding the spring TP provided no significant ($p < 0.05$) additional information to the equation.

To test the adequacy of this equation, we substituted the appropriate loads to predict the 1983 and 1984 spring TP, which were not used in the derivation of the equation. In each case, the predicted spring TP was within 5% of the observed concentrations.

Discussion

According to the multiple linear regression equation developed from the observed data, the TP load must decrease to 0.329

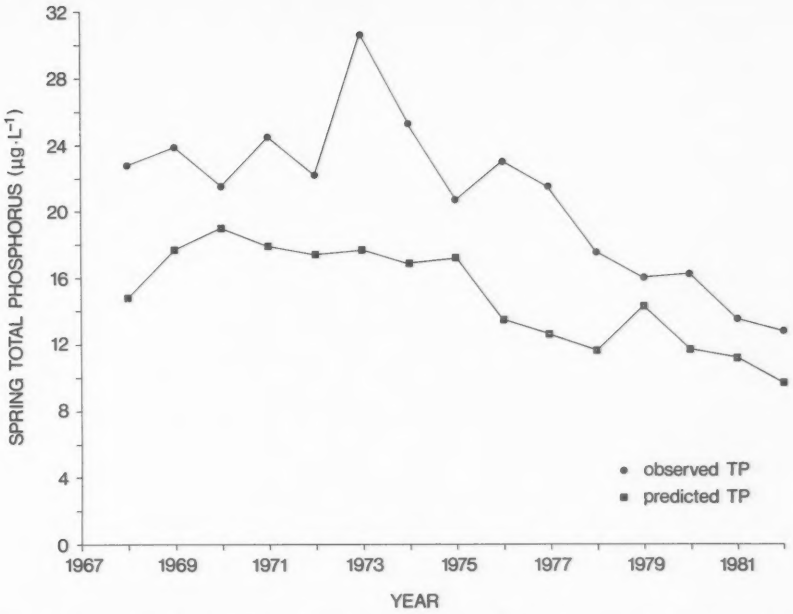

FIG. 7. Comparison of Vollenweider's (1976) predicted spring TP concentrations for Lake Ontario with observed concentrations.

$g \cdot m^{-2} \cdot yr^{-1}$ (~6230 $t \cdot yr^{-1}$) in order to achieve the target level of 10 $\mu g \cdot L^{-1}$. This is identical with the estimate of 0.33 $g \cdot m^{-2} \cdot yr^{-1}$, or 6260 $t \cdot yr^{-1}$), as determined using Vollenweider's (1976) "best" equation, based on OECD lakes. Current spring midlake TP concentrations are approaching the target level from a previous maximum of 30.6 $\mu g \cdot L^{-1}$ in 1973, indicating that measures for the reduction of ambient TP in Lake Ontario were clearly successful (Fig. 2). As expected, under nonequilibrium conditions, as when annual P loadings are constantly changing, predictions based on Vollenweider's steady-state model are considerably lower than observed concentrations (Fig. 7).

Chapra and Sonzogni (1979) estimated that it would require 7.8 yr to achieve a 90% response to a change in external load, while Thomann et al. (1977) estimated 10–20 yr. Lee et al. (1978) suggested that three times the P residence time (total in-lake mass/annual P load) would be necessary to achieve a new equilibrium TP concentration in response to a change in load. For Lake Ontario, this would be approximately 22 yr. Contrary to their predictions, our analysis indicates that 80% of the response of spring TP to loading changes occurs within 2 yr and 90% within 4 yr.

The relatively short response time observed for a water body of 1640 km^3 volume suggests that phytoplankton uptake and sedimentation play key roles in removing P from the lake. To determine the quantity of P retained in the lake, we compared the total load from 1972 to 1982, corrected for outflow losses through the St. Lawrence River to the change in in-lake mass. It was determined that for a TP load of 113 600 t, when 45 500 t is accounted for by outflow, 60%, or 68 100 t, was retained in the lake.

To investigate how the retention coefficient of Lake Ontario compares with more generalized predictions, we substituted our data into the Dillon and Rigler (1974a) equation developed to predict spring P concentrations:

$$[P_{spring}] = A(1\text{-}R) \cdot (zp)^{-1}$$

where A = P load (grams per square metre per year), R = retention coefficient of P, z = mean depth (metres), and p = fraction of lake volume lost annually through outflow. Rearranging and solving for R gives 0.6, or 60%, which is equal to that observed, demonstrating that, despite their size, large deep lakes such as Lake Ontario exhibit much the same degree of retention as other lakes.

Since the Niagara River contributes almost 40% of the TP load to Lake Ontario, while representing 85% of the total discharge to the lake, the forms of P in its inflow could have a profound influence on the fate of P in the lake. In examining data collected immediately offshore of the Niagara River mouth, it was found that, in general, particulate P accounts for greater than 50%, and up to 75%, of the TP load. Furthermore, nearly 20% of the river's TP load is contributed during the three strongly stratified months (July–September), which would serve to enhance the sedimentation of particulate matter. Lake Ontario has also been shown by satellite imagery to be strongly susceptible to $CaCO_3$ precipitation (Strong and Eadie 1978). Numerous studies have demonstrated the role of $CaCO_3$ precipitation in removing P from surface waters (Otsuki and Wetzel 1974; Koschel et al. 1983). In fact, Murphy et al. (1983) have suggested that coprecipitation of phosphates with $CaCO_3$ may strongly regulate biological activity. These factors would all serve to facilitate the rapid removal of P out of the water column.

The lack of a distinct trend in any of the algal biomass indicators from 1974 to 1982 suggests two explanations: either the statistical design of the program was insufficient to detect

the expected change in algal biomass or the biomass was not responding to the decrease in spring TP as predicted. Since Sakamoto (1966) first suggested there was a quantifiable relationship between chlorophyll and P in a number of Japanese lakes, an extensive volume of supportive literature describing similar relationships between mean summer chlorophyll and spring TP in northern temperate lakes has arisen (Dillon and Rigler 1974b; Vollenweider 1976; Rast and Lee 1978; Hickman 1980; Prepas and Trew 1983; Holmgren 1985). With such an overwhelming body of supporting evidence, and considering the rapidity of response of spring TP and the proportionally larger decrease of SRP to loading changes, it is expected that phytoplankton biomass would respond in a similar manner.

Knowlton et al. (1984) examined the sources of variability (field, daily, seasonal) in chlorophyll and P measurements for a number of lakes and their effects on the interpretability of data. They concluded that, with three samples per stratified period collected over 8 yr, one should be able to detect a twofold difference in chlorophyll between years with 90% confidence, or a 1.5-fold difference with 70% confidence. Since our database spanned 8 yr using a consistent methodology, the lack of a distinct trend appears to be a real phenomenon. Consequently, it is necessary to consider why the algal biomass failed to respond as predicted.

We first needed to determine whether existing P–Chl *a* models were applicable to large deep lakes such as Lake Ontario. After all, many of the studies were based on considerably smaller lakes, and in fact, Jones and Bachmann (1976) specifically excluded the Great Lakes from their analysis, reasoning that large lakes are incompletely mixed. This problem was addressed by Jones and Lee (1980) who, using the nutrient load – eutrophication response relationship developed for the U.S./OECD lakes (Rast and Lee 1978), demonstrated that deep lakes do exhibit the same response as shallow lakes.

While most P–Chl *a* relationships have been derived using spring TP concentrations, some studies have reported a stronger relationship using summer TP (Jones and Bachmann 1976; Forsberg and Ryding 1980; Prepas and Trew 1983; Gilliom 1984). Neilson and Stevens (1987) observed that point-source loadings of TP to Lake Ontario during the stratified period are sufficient to overcome losses from the epilimnion due to sedimentation. Under these conditions, it is reasonable to assume that algal populations are responding more to summer TP levels than spring levels. This assumption is further justified by the findings of Young and DePinto (1982) who reported that approximately 63% of the total particulate P in wastewater treatment plant effluents, and up to 35% of total particulate P in tributary inputs, is biologically available. Unfortunately, comparable summer TP and biomass data exist only for the period 1976–82. Nevertheless, we did not observe any significant relationship between summer TP and algal biomass. In addition, summer TP levels have, apart from 1976, exhibited a decrease of $<2\ \mu g \cdot L^{-1}$. The response of biomass to a change of this magnitude would be minimal compared with background variability.

The extremely high summer TP levels observed in 1976 might be expected to have led to elevated biomass values. These high TP levels, however, coincided with high water levels, suggesting that increased shoreline erosion, both in Lake Erie and Lake Ontario, was responsible. Since there is no biologically available P associated with bluff material (Young and DePinto 1982), the lack of a response in algal biomass is not unexpected.

We are attempting to detect a trend in algal biomass in response to a TP reduction of only $12\ \mu g \cdot L^{-1}$. The majority of P–Chl *a* relationships, however, have been developed from a large number of lakes, where the range of concentrations generally exceeded an order of magnitude. The effect of data range on the significance of the P–Chl *a* relationship was readily apparent from the work of Dillon and Rigler (1974b) who found that only after increasing the TP range from 11.2 to $177\ \mu g \cdot L^{-1}$ did they find a statistically significant relationship between spring TP and Chl *a*. Schindler (1978), in examining the IBP lakes plus the Experimental Lakes, concluded that he was able to find a significant TP–Chl *a* relationship because the data ranged over two to three orders of magnitude, so that the inherent variability of any one lake in the analysis would be rendered inconsequential in comparison. A similar conclusion led Smith and Shapiro (1981) to suggest that global models do not necessarily accurately predict the response of individual lakes because of the large variability of Chl *a* at any given TP concentration.

It is important, then, to consider those factors that may influence algal biomass other than TP levels. Nilssen (1978), in discussing the possible responses of water bodies subjected to recent eutrophication, suggested that a shift in phytoplankton species composition to larger forms is more likely to be observed than an increase in algal biomass. Schindler et al. (1973) reported that algal biomass was, to some extent, related to species composition, with populations dominated by green algae exhibiting a larger biomass than those dominated by blue-greens at similar P levels. Shifts in the dominant algal groups have been observed in Lake Ontario between 1970 and 1982. The contribution of Cyanophyta and Chrysophyta to total algal biomass during the stratified period appears to have declined from 20 to 30% in 1970 to less than 7% in 1982, based on the results of Johannsson et al. (1985), Gray (1987), and M. Munawar (CCIW, pers. comm.). In contrast, contributions from Diatomaceae and Dinophyceae have increased slightly from 10% to 10–20%. Unfortunately, no long-term information related to changes in algal species composition in Lake Ontario is available.

Chlorophyll content per cell volume can vary markedly both within and between species, further confounding any real trend in Lake Ontario algal biomass (Dolan et al. 1978; Hunter and Laws 1981; Lehman 1981; Granberg and Harjula 1982). This may account for the considerable variation in correlation coefficients observed between Chl *a* and both POC and PON during the stratified period, with r values ranging from 0.01 to 0.86. POC and PON, however, will also be affected by detritus, and therefore, it is not possible to differentiate between the two factors.

N:P ratios also alter species composition (Schindler 1977; Flett et al. 1980). Smith (1983, 1986) observed that, as the TN:TP ratio increases, there is a shift in dominance from blue-green to green algae and diatoms. Since 1972, the spring TN:TP ratio has increased from approximately 16 to greater than 35. Furthermore, midsummer TN:TP ratios in 1972 ranged from 12 to 14, suggesting that there may have been a seasonal shift from P to N limitation during the high-P years. In 1981 and 1982, summer TN:TP ratios were always greater than 20, with PON accounting for only 20% of TN, compared with 50% in 1972, indicating that N limitation could not occur. Smith (1986) did not differentiate between N-fixing and non-N-fixing forms in his analysis, reasoning that all blue-greens are good competitors for N. Data from Lake Ontario, however, suggest that the

decline in dominance was even greater for N-fixing blue-greens. Stoermer and Ladewski (1978) reported that nearly 80% of the blue-green algae in August 1972 contained heterocysts (i.e. were N-fixing), while in August 1982, there was almost a complete lack of heterocyst-containing cells (I. Gray, CCIW, pers. comm.).

A further factor that may be influencing algal biomass in Lake Ontario is the increasing number of planted salmonids. From 1968 to 1981, more than 27 million fish, including lake trout and coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*), have been planted in Lake Ontario by various fisheries agencies. In 1981 alone, 4.5 million fish were planted (Great Lakes Fishery Commission 1983). There is abundant evidence that alterations in fish communities can, under appropriate conditions, effect considerable changes in both algal biomass and species composition due to their predation of zooplankton (Morgan et al. 1978; Benndorf et al. 1984; Pace 1984). Both Shapiro and Wright (1984) and Reinertsen and Olsen (1984) reported marked reductions in algal biomass following the removal of planktivorous fish, independent of TP concentrations. Lake Ontario zooplankton community structure appears to be a consequence of intense planktivory by alewives (*Alosa pseudoharengus*) and appears unchanged since the late 1960's (Jonannsson et al. 1985; Taylor et al. 1987). There is no data spanning the period 1974–82, however, with which to assess whether algal biomass is being influenced by zooplankton predation.

In summary, P management strategies applied to Lake Ontario have been effective in reducing the annual TP load to the lake and, in turn, spring TP concentrations. The lack of a similar response in summer TP suggests that loading to the lake during the stratified period has not shown a similar decline and may be responsible for the lack of an observed trend in algal biomass indicators during this period. The extent to which other factors, such as changes in algal community composition or zooplankton predation or increases in N levels, may be confounding this trend, however, cannot be evaluated due to a lack of data.

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Phosphorus Deficiency of Lake Ontario Plankton

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Lean, D. R. S., A. A. Abbott, and F. R. Pick. 1987. Phosphorus deficiency of Lake Ontario plankton. Can. J. Fish. Aquat. Sci. 44: 2069–2076.

The phosphate deficiency index (PDI), the ratio of photosynthetic carbon assimilation at optimal light to the maximum uptake velocity for phosphate, showed that P deficiency occurred in the nearshore plankton of Lake Ontario during spring thermal bar conditions and in the midlake plankton immediately after stratification. This condition persisted until October, when deep mixing of the water column occurred. Carbon and phosphate assimilation were by similar size classes, and as the ratio of two rate processes, PDI was independent of both temperature and biomass. Turnover time and alkaline phosphatase activity (APA) correlated with PDI. Short-term photosynthetic depression with phosphate enrichment occurred in only 7 of 23 experiments and may either reflect P-sufficient conditions or high protein to carbohydrate ratios due to physical events common to large lakes. PDI, protein to carbohydrate ratios, and photosynthetic depression respond principally to algal activity. Although turnover time and APA reflect the activity of smaller microorganisms, primarily heterotrophic bacteria, all indices were consistent.

L'indice de déficience en phosphate (IDP), soit le rapport entre le taux d'assimilation photosynthétique du carbone à un niveau de luminosité optimal et la vitesse de captation maximum du phosphate, montre qu'une déficience en P a lieu chez le plancton côtier du lac Ontario quand la thermocline est présente au printemps et chez le plancton semi-hauturier immédiatement après la stratification. Cette condition a duré jusqu'en octobre quand un mélange profond de la colonne d'eau a eu lieu. Le carbone et le phosphate ont été assimilés par le plancton de classes de taille semblable et, à titre de rapport de deux procédés à taux de transfert, l'IDP était indépendant de la température et de la biomasse. Le temps de renouvellement et l'activité de la phosphatase alcaline (APA) étaient en corrélation avec l'IDP. Une dépression photosynthétique à court terme liée à l'enrichissement au phosphate a eu lieu au cours de 7 des 23 expériences; ceci peut traduire une quantité suffisante de P ou des rapports élevés entre les teneurs en protéines et en hydrates de carbone à cause d'événements physiques typiques de grands lacs. L'IDP, les rapports protéines–hydrates de carbone et la dépression photosynthétique réagissent surtout à l'activité algale. Quoique le temps de renouvellement et l'APA reflètent l'activité de petits micro-organismes, surtout des bactéries hétérotrophes, tous les indices étaient uniformes.

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Lake monitoring over intervals of weeks and months has been used traditionally in a vain attempt to find seasonal patterns between plankton biomass and available phosphate concentrations. The interpretation of such data is complicated because values for soluble reactive phosphate (SRP) are often near detection limits, may overestimate biologically available phosphate (Rigler 1973), and do not include phosphate stored by algae (Lean et al. 1983). Spring SRP in Lake Ontario has dropped by 70% since 1972, and spring total P concentration in 1982 was half that found in the early 1970s. However, midlake summer total P and chlorophyll have not changed. In fact, summer epilimnetic total P concentration now exceeds spring P and summer hypolimnetic total P (Stevens and Neilson 1987). These observations illustrate some of the unusual features that complicate the Lake Ontario P cycle.

Experiments with radioactive phosphate have shown that all of the phosphate in epilimnetic waters may be taken up and replaced in minutes (Rigler 1973; Lean et al. 1983; present study). Subcellular distribution patterns of recently assimilated radioactive phosphate suggest that, in 1982, the plankton present in Lake Ontario were P deficient to some degree during the entire season (Lean and Cuhel 1987). Alkaline phosphatase activity (APA) also indicated that the nanoplankton were P deficient, but only during the summer stratified period (Pick 1987a). The ratio of protein to carbohydrate, another index of P deficiency, changed little throughout the season and usually remained above the level expected for P-limited plankton (Pick 1987b).

In the following investigation, the P deficiency index (Lean and Pick 1981), phosphate turnover time, and the photosynthetic

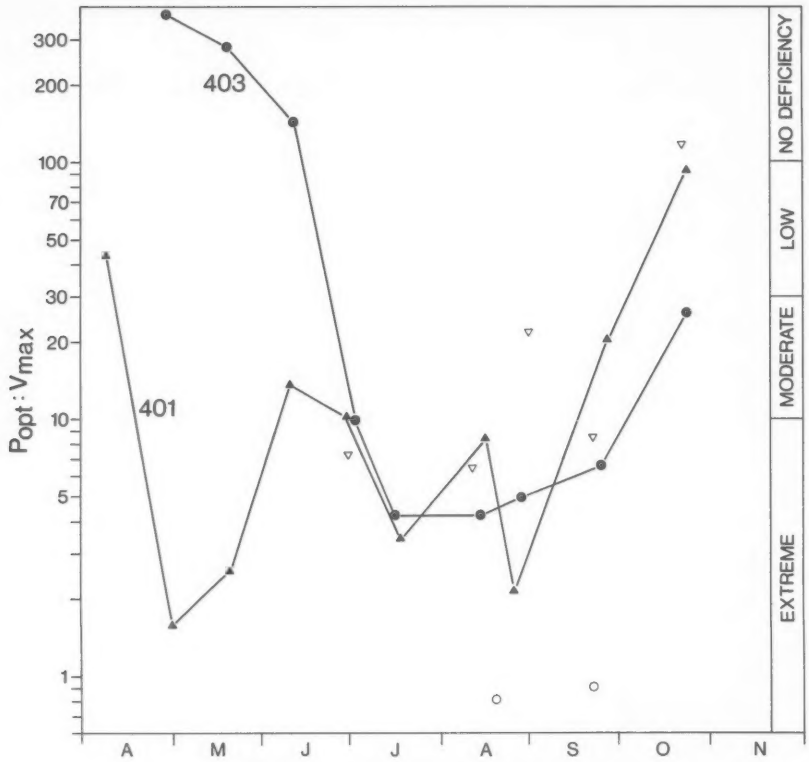

FIG. 1. $P_{opt}:V_{max}$ ratio (=PDI) for stations 401 (▲) and 403 (●) with additional data for station 405 (▽) and Jacks Lake (○). On the right is the arbitrary scale for phosphate deficiency.

depression following nutrient enrichment were used to assess the degree and duration of P-deficiency of the plankton populations in Lake Ontario during 1982.

Methods

The ratio of photosynthetic C assimilation measured at optimal light (P_{opt}) to the maximum uptake velocity for phosphate (V_{max}) has been termed the phosphorus deficiency index (PDI) by Lean and Pick (1981) and Lean et al. (1983). Values near 100 indicate no deficiency and are characteristic of balanced growth conditions. Values of 30–100 indicate a low level of P-deficiency, 10–30 moderate, and below 10 extreme P deficiency. Luxury consumption of phosphate by phosphate-deficient plankton can cause phosphate uptake rates to be equivalent to C assimilation rates.

Phosphate turnover time is determined using carrier-free ^{32}P–PO_4. This is the time required for an amount of phosphate to be taken up equivalent to that present. A value of 1–10 min would indicate high P deficiency whereas turnover times of days are found when conditions of no P deficiency exist.

Photosynthetic depression has been observed following phosphate additions to P-deficient populations (see Healey 1979; Lean and Pick 1981). Growth is suppressed under P limitation and the products of photosynthesis accumulate principally as carbohydrate. The response to a phosphate increase is a temporary (1–4 h) reduction in C fixation as energy is shifted to phosphate assimilation and storage of polyphosphate. During measurements of primary production, replicate samples were enriched with phosphate (1 μM) and incubated under identical conditions. Values less than 90% of the control were considered significantly depressed.

Samples were obtained at a northshore station (401), a midlake station (403), and a southshore station (405) along a north–south transect from near Cobourg, Ontario (Lean 1987; Simons and Schertzer 1987). Samples were occasionally collected at Jacks Lake, where an even greater degree of nutrient deficiency has been observed (Lean and Pick 1981; Pick et al. 1984; Lean and Cuhel 1987) even though the total P and chlorophyll levels are similar to Lake Ontario.

Phosphate turnover time was measured by adding sufficient carrier-free ^{32}P–PO_4 (Amersham or New England Nuclear) to 200–300 mL of freshly collected lake water to give a final concentration of 5000–50 000 dpm·mL^{-1} depending on the expected percent incorporation. Results with either glass of polycarbonate bottles were the same; the latter were used most often because of less chance of breakage. Subsamples (5–10 mL) were removed at intervals appropriate for the rates measured and the particulate material collected on 0.2-μm Nuclepore filters. Little water is retained using these filters compared with the commonly used cellulose nitrate or glass fiber filters, and consequently, washing the filters to remove residual activity was unnecessary except when turnover times exceeded 100 h. After 1–3 h, samples were also filtered on 1-,

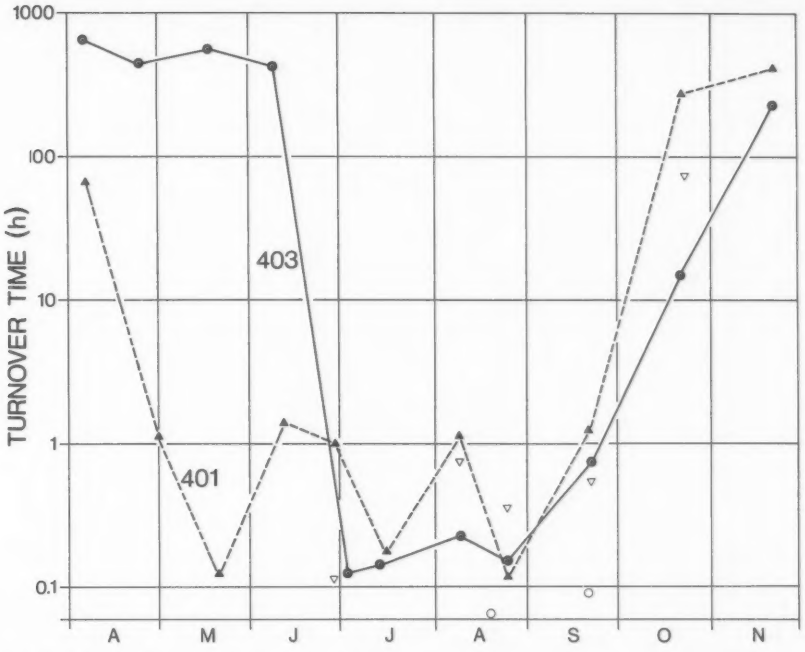

FIG. 2. Phosphate turnover time for stations 401 (▲) and 403 (●) with additional data for station 405 (▽) and Jacks Lake (○).

5-, and 12-μm Nuclepore filters. Filters were first solubilized using 100 μL of 10:1 methylene chloride and ethanolamine, and 10 mL of PCS (Amersham) fluor was then added for liquid scintilation counting. The slope of the natural logarithm of the percent ^{32}P in the filtrate was regressed against time and the initial slope used to approximate the uptake rate constant. R values were always in excess of 0.90 and usually near 0.99. The turnover time of phosphate is the reciprocal of the rate constant.

Rate constants were also measured at elevated phosphate and used to estimate V_{max}. Generally, V_{max} was reached at additions of about 10 μg $P \cdot L^{-1}$. Ambient concentrations were negligible compared with added phosphate. P_{opt} was obtained by measuring uptake of [^{14}C]bicarbonate (Amersham) at five light levels for 2–4 h. Samples were collected on 0.2-, 1-, 5-, and 12-μm Nuclepore filters and processed as above. Values obtained on 1-μm Nuclepore filters compared well with those of Cuhel and Lean (1987b) who used GF/F filters for subcellular fractionation of the assimilated ^{14}C. The P_{opt} to V_{max} ratio provides the PDI described by Lean and Pick (1981).

Results

Phosphate Deficiency Index

At the midlake station, 403, values of the PDI exceeded 100 from April to the end of June (Fig. 1). Presumably, these extremely high ratios indicate that the C fixed, in excess of that required for balanced growth (i.e. PDI = 100), was necessary to support respiration, as the water column mixed to the bottom (178 m) leaving the plankton in the dark for much of the time. In May–June, SRP values were about 4 μg $P \cdot L^{-1}$, so no deficiency was expected.

At the northshore station, 401, P deficiency was observed inside the thermal bar in April and May (Fig. 1). In fact, the greatest deficiency observed in Lake Ontario using the PDI index was at 401 at the end of April. As the thermal bar widened and deepened in May and June (Simons and Schertzer 1987), some relaxation of the deficiency was observed.

When the entire lake stratified late in June, values at the northshore, southshore, and midlake stations were similar. At station 403, the plankton showed extreme phosphate deficiency throughout the rest of the summer. The PDI at the northshore and southshore stations was more variable, perhaps due to wind-induced currents and upwelling events discussed by Simons and Schertzer (1987).

As the epilimnion deepened in September and October the PDI moved into the moderate and low levels of deficiency. When the entire water column mixed at the nearshore stations (38 m) the plankton was no longer deficient. Moderate deficiency continued through November at 403. Although the mixing depth had increased to about 40 m, the water column remained stratified. For comparison, two examples from Jacks Lake (Fig. 1) exhibited a greater P deficiency than samples from Lake Ontario.

Phosphate Turnover Time

Seasonal changes in phosphate turnover time (Fig. 2) ranged over 4 orders of magnitude (0.6–600 h). During the period of deep mixing, turnover times at 403 were in excess of 400 h. The decline in June was probably more rapid than shown because stratification occurred within 2–3 d at the end of June (Simons and Schertzer 1987). Cruise temperature data also showed a rapid increase from 5.8°C on 29 June at station 403 to 12°C on 2 July. During July and August the turnover time at 403 remained

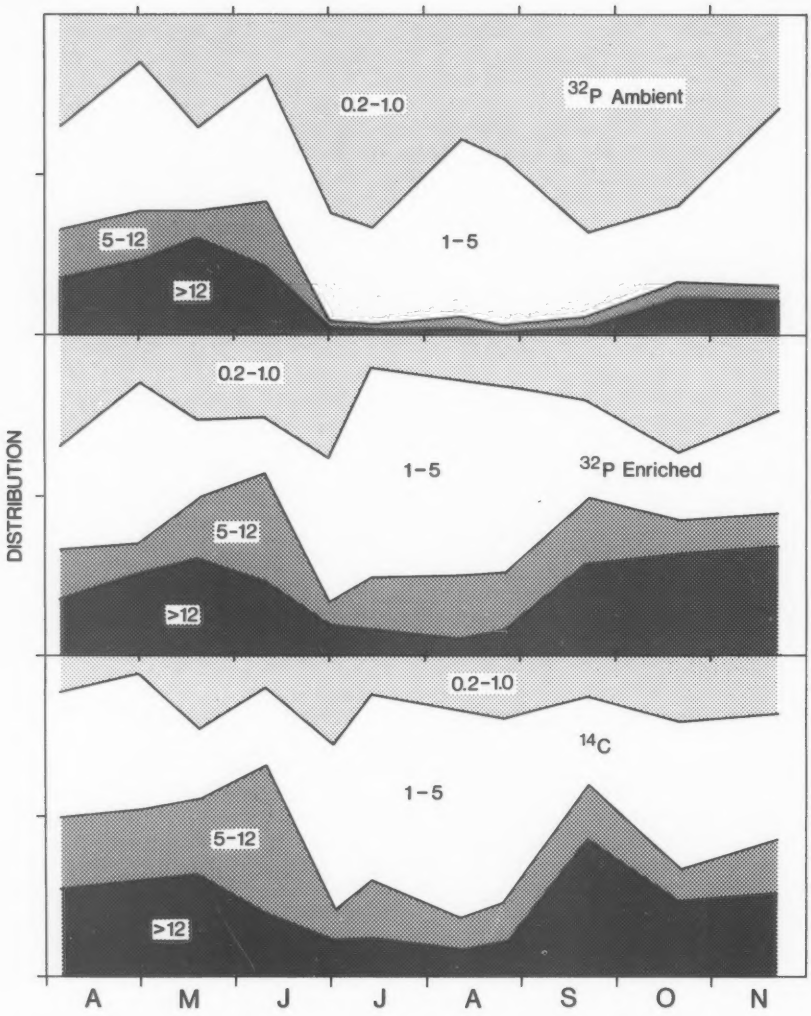

FIG. 3. Size distribution (classes in μm) of uptake of (top panel) carrier-free $^{32}P–PO_4$, (middle panel) phosphate enriched, and (bottom panel) assimilated [^{14}C]bicarbonate for station 403.

rapid (12 min), slowing to 20 h in October and in excess of 100 h in November.

At the northshore station, turnover times became rapid as the thermal bar developed in April. Although the temperature on 30 April was only 2.7°C, the turnover time was much more rapid (1 h) than at the midlake station (560 h). By 20 May, values had declined to 7 min. As with the PDI (Fig. 1), the turnover time relaxed to 1 h in June as the thermal bar widened and deepened. In the summer, the turnover time was generally slower at the northshore and southshore stations than at the midlake station. Turnover times for the samples obtained from Jacks Lake during August and September were less than any observed in Lake Ontario (Fig. 2).

The size distribution of uptake of radioactive phosphate illustrates that turnover time should not be normalized for biomass differences (as in Sproule and Kalff 1978). When turnover times exceeded 400 h, the uptake by the 0.2–1 μm fraction was only about 25% of the carrier-free $^{32}P–PO_4$ (Fig. 3, top panel). In summer, uptake by this fraction often exceeded 60% but returned to 30% in fall. The decline observed in August followed the upwelling event discussed above. Direct enumeration (Caron et al. 1985; Pick and Caron 1987) confirmed that about 90% of the bacteria and some of the picocyanobacteria were in this fraction.

The seasonal pattern in the size distribution of uptake of carrier-free radioactive phosphate was different from that for carbon (Fig. 3, bottom panel) during summer. With phosphate enrichment (middle panel) the distribution of P and C uptake was similar. For both elements, the uptake by the >5 μm fraction was 40–60% in spring and fall with summer values near 20%. Corresponding values for >5 μm fraction in the non-enriched sample were near 5% in the summer. The above

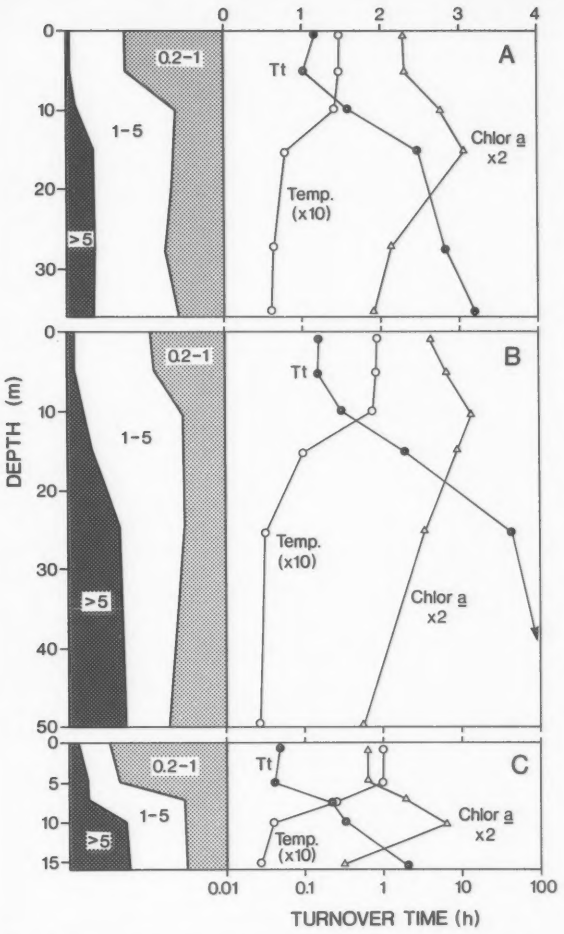

FIG. 4. Distribution of carrier-free ^{32}P–PO_4 (on left) expressed as a function of depth. On the right is temperature (scale × 10 = °C), chlorophyll *a* ($\mu g \cdot L^{-1}$), and phosphate turnover time on log-scale at the bottom for (A) station 401 on 24 August, (B) 403 on 12 August, and (C) Jacks Lake on 17 August 1982.

observations show that the PDI was calculated from a ratio derived from C and P uptake by similar sized organisms whereas the uptake of carrier-free phosphate was mainly by picoplankton during the P-deficient periods. Larger cells obtain phosphate only when elevated concentrations of phosphate are encountered (Lean 1984; this study).

The size distribution of ^{32}P uptake, turnover time, temperature, and chlorophyll *a* are shown as a function of depth (Fig. 4) during periods of extreme P deficiency at stations 401 and 403 and Jacks Lake. At all depths, SRP values were at the detection limit of 0.2 $\mu g\ P \cdot L^{-1}$ except at 25 and 50 m at 403 where values increased to 0.6 and 0.7. Consequently, SRP provided little information on the nutrient status of the population. Changes in chlorophyll *a* were small, so differences in uptake were not due to large differences in algal biomass. However, turnover times varied over 3 orders of magnitude, increasing from 6 to 14 min in the epilimnion where only a small fraction (<10%) of the uptake was by particles >5 μm. Below the epilimnion the turnover time increased as the percent incorporation by the >5 μm fraction increased. Despite similar P and chlorophyll concentrations, the turnover time was faster in Jacks Lake. While the depth of the epilimnion was similar to that at 401, the physical activity was greater. The stable thermal structure of Jacks Lake may act as a more effective barrier for vertical transport of P.

PDI values were also obtained at Jacks Lake and station 403 at the depths shown on Fig. 4 and are compared with temperature and turnover time (Table 1). For Jacks Lake the PDI remained in the range expected for extreme P deficiency whereas at 403, values increased from moderate at the surface to low at 50 m. Although the surface turnover times were the same, the PDI showed that Jacks Lake was more P deficient, largely due to the higher V_{max}. At 15 m the Jacks Lake turnover time was long (11.2 h) but the PDI remained low. Both increased in the metalimnion but the turnover time increased more.

Turnover times were measured as a function of depth in Lake Ontario throughout the study period. Generally, rapid turnover times were found only in the epilimnion of well-stratified water columns. Turnover times were longer in the metalimnion, and only at these times was appreciable uptake of carrier-free ^{32}P–PO_4 found in the larger fractions.

Photosynthetic Depression

Photosynthetic depression with phosphate enrichment was observed in only 7 of 23 experiments (Table 2). Healey (1979) predicted photosynthetic depression when the protein to carbohydrate ratio was less than 0.7. Using data from Pick (1987b), five of the seven experiments that showed photosynthetic depression with phosphate enrichment had ratios equal to or less than 0.7. When the protein to carbohydrate ratio exceeded 0.7, only two exhibited photosynthetic depression. Therefore, Healey's hypothesis predicted the response in 19 of the 23 experiments. Photosynthetic depression has been observed repeatedly in Jacks Lake (Lean and Pick 1981) where protein to carbohydrate ratios were also considerably lower than in Lake Ontario (Pick 1987b).

Discussion

A suitable physiological indicator of P deficiency requires a rate measurement that can be made before the reaction conditions change appreciably. This is especially critical for a transport reaction, for both external and internal concentrations of phosphate can contribute to the regulation of transport capacity (e.g. see Rhee 1980). Rates must be determined (1) before added phosphate or its metabolic products exert allosteric inhibition, (2) before the added phosphate is depleted to an extent detectable by the transport system, or (3) the population is altered through growth, death, or inhibition.

Although some doubt exists that reliable primary productivity measurements can be made in closed containers, our values were reproducible, and rates were constant over incubation times of 0.5–3 h or more (Lean and Knowles 1987; Cuhel and Lean 1987b). Uptake velocity was measured from time course experiments, so PDI meets the above criteria. Likewise, phosphate turnover time, calculated from the initial slope of the uptake of ^{32}P–PO_4 would be an acceptable physiological indicator of P deficiency. Turnover times provide an integrated measure of transport capacity of the plankton assemblage and ambient phosphate concentration. These two methods differ in

TABLE 1. Comparison of phosphate turnover time (TT) and the phosphate deficiency index (PDI) as a function of depth during thermal stratification.

Depth (m)	Temp. (°C)	TT (h)	V_{max} ($\mu g\ P \cdot L^{-1} \cdot h^{-1}$)	P_{opt} ($\mu g\ C \cdot L^{-1} \cdot h^{-1}$)	PDI ($\mu g\ C : \mu g\ P$)
			Jacks Lake, 17 August 1982		
1	20.1	0.07	4.93	5.8	1.2
5	20.0	0.06	4.84	6.1	1.3
7.5	15.2	0.17	5.09	6.2	1.2
10	7.0	0.31	2.73	6.4	2.4
12.5	5.6	0.51	1.07	2.4	2.2
15	5.0	11.2	0.75	2.4	3.3
			Station 403, 26 August 1982		
1	12.5	0.07	0.83	9.8	11.8
5	12.5	0.08	0.81	11.1	13.7
10	12.4	0.09	0.54	8.2	15.1
15	12.0	0.11	0.30	4.8	15.9
25	4.8	2.10	0.15	2.8	19.3
50	4.2	24.51	0.03	1.7	51.5

TABLE 2. Comparison of protein to carbohydrate ratio with optimum photosynthetic rate (P_{opt}) and the percent of (P_{opt}) with added phosphate (1 μM) for stations 401, 403, and 405 and Jacks Lake in 1982.

Date	P_{opt} ($\mu g\ C \cdot L^{-1} \cdot h^{-1}$)	%	Protein to carbohydrate ratio
Station 401			
7 Apr.	8.6	95	1.8
30 Apr.	10.4	103	1.5
20 May	3.0	105	1.4
8 June	4.0	93	1.5
30 June	16.4	93	1.2
15 July	5.4	95	0.7
12 Aug.	5.4	98	1.0
24 Aug.	9.3	95	1.0
Station 403			
28 Apr.	2.4	103	1.7
18 May	2.9	96	1.6
11 June	4.3	96	1.5
2 July	29.6	92	1.6
13 July	13.5	74	0.7
11 Aug.	9.3	81	2.0
25 Aug.	9.5	97	1.3
23 Sept.	10.8	58	0.6
20 Oct.	6.6	102	0.9
Station 405			
1 July	25.1	96	1.2
11 Aug.	10.2	75	1.4
21 Sept.	9.4	65	0.6
19 Oct.	13.0	103	0.9
Jacks Lake			
18 Aug.	6.4	68	0.3
21 Sept.	4.6	45	0.5

that turnover time is measured under ambient conditions, and PDI or more specifically V_{max} is measured under enriched conditions. The capacity for P uptake is in turn related to P deficiency. A second difference is that turnover time is most strongly influenced by the picoplankton, but the plankton size that assimilates P at V_{max} is also responsible for C assimilation at P_{opt}. Because PDI is a ratio of two temperature-dependent rate measurements, the influence of temperature and biomass is normalized. PDI is largely influenced by changes in V_{max} which covered several orders of magnitude (0.006–6.52 $\mu g\ P \cdot L^{-1} \cdot h^{-1}$), while P_{opt} values ranged from 1.6 to 26.0 $\mu g\ C \cdot L^{-1} \cdot h^{-1}$. This means that PDI has the advantage of V_{max}, as suggested by Sproule and Kalff (1978), Healey (1979), Vincent (1981),and Zevenboom et al. (1982), but is normalized for temperature and biomass differences.

Temperature and microbial biomass have a greater effect on turnover time. Picoplankton are largely responsible for the rapid turnover time at 5 m, and these diminished with depth in the metalmnion (see station 403, 12 August, in Pick and Caron (1987), their fig. 8b). Consequently, only the larger plankton remain at these depths and they are unable to deplete phosphate sufficiently to cause rapid turnover. Whether uptake by small cells is the cause or the consequence of rapid turnover times remains unresolved.

The proportion of the uptake of [^{14}C]bicarbonate and enriched ^{32}P–PO_4 (Fig. 3) by the 0.2–1.0 μm fraction was similar. This requires that either the [^{14}C]bicarbonate was quickly transferred to the $<1\ \mu m$ fraction or was directly assimilated by the $<1\ \mu m$ fraction. If the latter was correct, little uptake of phosphate was by heterotrophic bacteria.

PDI, turnover time, and APA have been used separately as indicators of P deficiency in plankton but rarely have they been compared. Only Sproule and Kalff (1987), Healey (1979), and Vincent (1981) used several physiological indicators concurrently. For a variety of reasons, one might expect differences between PDI and turnover time. However, the seasonal patterns were similar (Fig. 1 and 2) and they correlated quite well (Fig. 5). Data were collected over a wide range of temperatures (1–23°C), chlorophyll concentrations (1–10 $\mu g \cdot L^{-1}$), primary productivity (2–30 $\mu g\ C \cdot L^{-1} \cdot h^{-1}$), and species composition (Gray 1987; Pick and Caron 1987). One data point showing poor fit was from station 401 on 28 April when the thermal bar had only recently formed; the colder temperature may have caused turnover time to be low. Another datum which correlated poorly was obtained following the August upwelling event. At this time, APA also indicated lower deficiency than PDI.

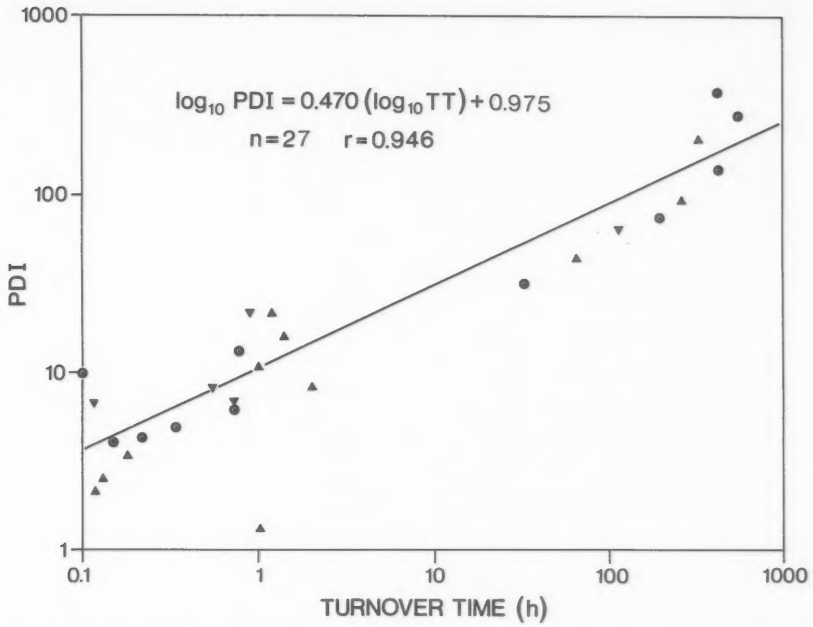

FIG. 5. Phosphate deficiency index (PDI) as a function of turnover time for stations 401 (▲), 403 (●), and 405 (▼).

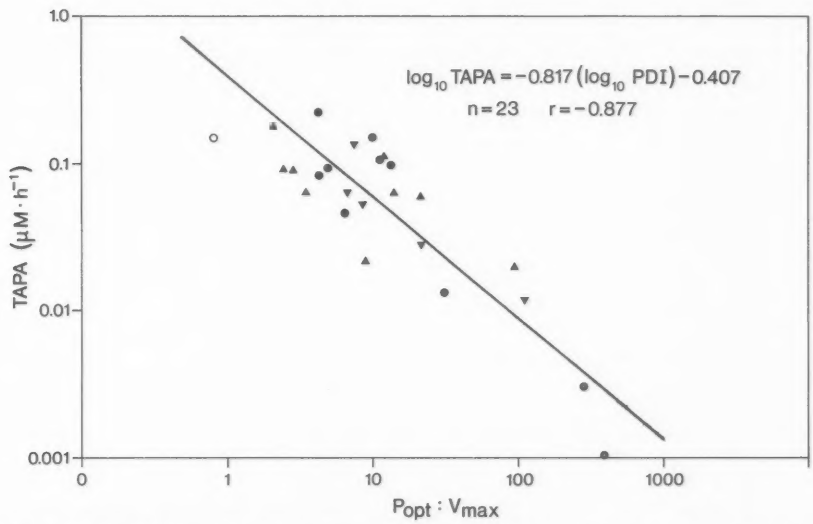

FIG. 6. Relationship between the PDI and total alkaline phosphatase activity (TAPA) in Lake Ontario for stations 401 (▲), 403 (●), and 405 (▼). Jacks Lake value (○) was not included in the regression.

APA was measured in Lake Ontario (Pick 1987a) on samples taken along with those for PDI and turnover time estimates. On a linear scale, there was a weak negative correlation between total APA and PDI ($n = 22$, $r = -0.52$). The relationship was worse when particulate APA or APA normalized for chlorophyll *a* was used. When the data were log-transformed the relationship of total APA and PDI was highly significant (Fig. 6). Increases in PDI were accompanied by decreases in total APA. A single measurement from Jacks Lake (Fig. 6) suggests that this relationship may be different for each lake. Jacks Lake showed extreme P deficiency as measured by PDI (Lean and Pick 1981; Pick et al. 1984; this study) but here, APA was low relative to APA in Lake Ontario.

Discrepancies existed between APA (Pick 1987a) and PDI (Fig. 1) on specific dates. At stations 401 and 403, peaks of high APA were measured in early July and late August but APA was

depressed in the middle of August. Values for PDI indicated extreme P deficiency all summer long. One explanation for this difference is that APA was found to be a function of microbial biomass <20 μm (Pick 1987a), while the PDI as the ratio of two rate measurements (both biomass dependent) was not. During mid-August, microbial biomass was depressed at 401 and 403 (Pick and Caron 1987) due to an upwelling event at the northshore (Simons and Shertzer 1987). This would also tend to increase the relative size of the plankton.

The protein to carbohydrate ratio has also been used as an indicator of plankton nutritional status (see review in Pick 1987b). According to Healey (1979), severe N or P deficiency results in protein to carbohydrate ratios below 0.7. In Lake Ontario, ratios reached a low of 0.7 only in mid-July, September and November (Table 2). Ratios for the rest of the summer were above 1 or higher which indicates no nutrient deficiency. In late August, values were above 1.2 at 401 and 403, when APA was at its highest but PDI was between 2 and 8. In November at 401, the ratio dropped to 0.7 when neither APA nor PDI suggested any nutrient deficiency. This November value was interpreted as resulting from entrainment of hypolimnetic water which by the end of summer was low in protein and high in carbohydrate (Pick 1987b). As a result, in Lake Ontario, the protein to carbohydrate ratio showed the poorest agreement with the other indicators of P deficiency. Jacks Lake protein to carbohydrate ratios were well below 0.7 (and as low as 0.3) during the summer when PDI values were below 1 (Fig. 1).

Several additional factors aside from nutrient status may influence the ratio of protein to carbohydrate. One is the average light levels in the euphotic zone. Proportionally more protein is synthesized at low light levels than carbohydrate (Cuhel and Lean 1987a, 1987b); therefore, protein to carbohydrate ratios might be higher in a deep mixing population or as a consequence of upwelling of metalimnetic populations. Diurnal changes in the ratio were observed (Pick 1987b) that could be the result of changing light levels and/or changing patterns of zooplankton grazing.

Photosynthetic depression following phosphate enrichment occurred in only 5 of 21 experiments conducted in Lake Ontario but was shown to correspond to high protein to carbohydrate ratios. This may have resulted from episodic physical events in Lake Ontario which either bring fresh P to the epilimnetic population or upwelling of phytoplankton growing at greater depths.

All indicators (PDI, turnover time, APA, protein to carbohydrate ratios, and photosynthetic depression) point to the same conclusion. Plankton were P deficient at station 401 during thermal bar conditions but the midlake station did not become deficient until summer stratification. Upwelling events reduce the degree of P deficiency, particularly along the north shore.

Acknowledgments

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Subcellular Phosphorus Kinetics for Lake Ontario Plankton

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The subcellular distribution of recently incorporated $^{32}PO_4$ was used to demonstrate that plankton in the surface waters of Lake Ontario were phosphorus deficient to some extent throughout the entire study period from April to October 1982. Most (~80%) of the initial uptake of carrier-free radioactive PO_4 was in the low molecular weight (LMW) fraction. Ribonucleic acid (RNA) was the other major fraction. Although uptake was often complete within 1 h, changes in the subcellular distribution continued for 6–20 h with about half the LMW^{32}P being transferred to RNA. Both a phospholipid fraction and a fraction extracted with hot trichloroacetic acid (HTCA) containing DNA and high molecular weight polyphosphate increased to 4–15% of the total isotope incorporated. In contrast with these experiments where net P uptake was zero, with added PO_4 the net influx continued for periods in excess of 30 h but the subcellular distribution was constant within 2–4 h. About 80% of the initial uptake was as LMW^{32}P and a rapid net synthesis of LMW polyphosphate was observed. These patterns were common for both small and large plankton size classes.

La distribution subcellulaire du $^{32}PO_4$ récemment incorporé a servi à démontrer que le plancton des eaux superficielles du lac Ontario a manqué de phosphore jusqu'à un certgain degré pendant la période expérimentale, soit d'avril à octobre 1982. La plus grande partie (~80%) du phosphate radioactif libre initialement capté appartenait à la fraction de faible poids moléculaire tandis que l'acide ribonucléique (ARN) constituait l'autre principale fraction. Quoique la captation était souvent complète en deça de 1 h, la distribution subcellulaire a continué à varier pendant 6 à 20 h; ainsi, environ la moitié du ^{32}P de faible poids moléculaire a été transféré à l'ARN. La fraction phospholipidique, la fraction contenant de l'ADN extraite à l'acide trichloroacétique chaud (HTCA) et la polyphosphatase de poids moléculaire élevé ont augmenté pour constituer de 4 à 15 % du total des isotopes incorporés. Par opposition aux expériences où la captation nette de P s'élève à zéro, l'afflux net s'est poursuivi pendant plus de 30 h après l'ajout de phosphate mais la distribution subcellulaire est devenue constante après 2 à 4 h. Environ 80 % de la captation initiale concernait le ^{32}P de faible poids moléculaire et on a observé une synthèse nette rapide de la polyphosphatase de faible poids moléculaire. Ces régimes étaient communs chez le plancton de petite et de grande tailles.

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Annual phosporus loading estimates have been used in whole-lake models to predict average summer chlorophyll concentrations and hypolimnetic oxygen depletion rates (Vollenweider and Kerekes 1981), but short-term kinetic experiments have identified rapid turnover of various soluble and particulate P compartments (Rigler 1973; Lean 1973, 1984; Taylor and Lean 1984; and others as reviewed by Cembella et al. 1984a, 1984b). Such observations have led to P deficiency indices for predicting the duration and degree of P limitation in lakes (Lean and Pick 1981; Lean et al. 1987). The present investigation extends our knowledge of plankton P metabolism to the subcellular level under both ambient and P-enriched conditions.

Under extreme P deficiency, turnover times for dissolved orthophosphate are very short (~10 min). Isotopic equilibration of the various particulate and dissolved compartments occurs with carrier-free radioactive PO_4 without any net increase in particulate phosphate. Influx is equal to efflux as P is simply exchanged between the particulate and dissolved forms (Lean and White 1983). However, since P-deficient plankton can rapidly assimilate PO_4 when it becomes available (Lean et al. 1987), experiments with added PO_4 illustrate patterns for net uptake and storage.

Phosphorus is an integral component of a number of biological macromolecules, principally ribonucleic acid (RNA), deoxyribonucleic acid (DNA), and membrane lipids, and can be stored as polyphosphates in microorganisms (Harold 1966; Healey 1973; Rhee 1980; Cembella et al. 1984a, 1984b). Nucleotides such as adenosine triphosphate (ATP) and other high-energy P compounds provide the energy for most biosynthetic processes (protein, RNA, DNA, and lipid synthesis; contractile processes; active transport of elements). ATP is generated via substrate-level or oxidative phosphorylation and photophosphorylation. Unlike other inorganic nutrients (e.g. SO_4, NO_3, NH_4, CO_2), PO_4 enters the planktonic food web through autotrophic and heterotrophic microorganisms. It is made available for macromolecular synthesis or energy metabolism by esterification to organic carriers (ADP, glucose, etc.).

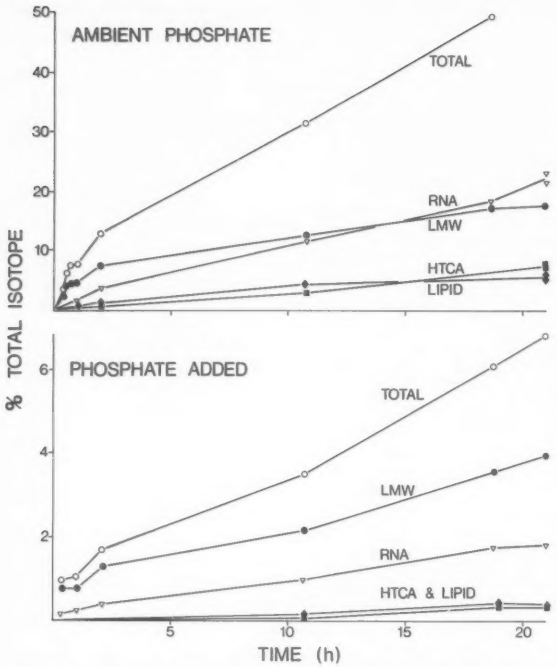

FIG. 1. Isotope uptake expressed as a percent of total added radioactivity (○) and in LMW (●), RNA (▽), lipid (◆), and HTCA (■) as a function of incubation time.

The high-energy intermediates thus produced are used for all other P-utilizing reactions. Phosphate differs from the other inorganic nutrients in that it rarely undergoes biological reduction to form C—P bonds (Kittredge and Roberts 1969). Almost all P-containing compounds are phosphate esters.

Animals lack the ability to take up soluble P directly and they excrete excess PO_4 (Rigler 1973; Taylor and Lean 1984), but the fraction excreted depends on the C:P ratio in the food. At C:P ratios in excess of 140, zooplankton may become P limited (Olsen et al. 1986). In the following investigation the influence of zooplankton is insignificant, for little labelling occurs during the experimental period.

A detailed kinetic analysis of the P pathways in even a single organism has been elusive (Cembella et al. 1984b). Consequently, an attempt to measure subcellular metabolism for an entire plankton population would seem fanciful. Nevertheless, the distribution of recently acquired radioactive PO_4 provides an operational classification of the P nutritional state of the plankton community. In the following experiments, the criterion used for P deficiency was that PO_4 additions to P-sufficient plankton populations should not alter the labelling patterns of subcellular distribution of recently incorporated $^{32}PO_4$. A shift to P storage would suggest that the population was P deficient. Changes in subcellular distribution of radioactive P were monitored with and without added PO_4 during the summer of 1982 in Lake Ontario.

Materials and Methods

Samples were collected at stations 401 and 403 (Lean 1987; Simons and Schertzer 1987) in Lake Ontario and compared with samples from Jacks Lake, a smaller lake of similar trophic state on the edge of the Canadian Shield (Lean and White 1983). Carrier-free $^{32}PO_4$ with or without unlabelled PO_4 (25–35 $\mu g\ P \cdot L^{-1}$) was added to steam-cleaned glass or polycarbonate bottles filled with water from 5 m depth. Final activities were about 40 000 (no added P) to 100 000 (with added P) $dpm \cdot mL^{-1}$. Soon after isotope addition and at intervals thereafter, 10-mL subsamples were filtered through Whatman GF/F filters and rinsed with 5 mL of filtered lake water. The cell-retaining portion of the filter was excised using a punch funnel and then frozen immediately (Cuhel et al. 1983).

Samples were treated by serial extraction to separate subcellular fractions. Filters were ground in cold 10% trichloroacetic acid (TCA), centrifuged (5000 × *g*, 20 min), and the residue rinsed with 10% TCA, yielding the low molecular weight (LMW) fraction which contains orthophosphate, pyrophosphate, short-chain polyphosphates (PolyP a), and a wide variety of organic phosphate esters such as sugar phosphates, nucleotides, etc.

The residue was then extracted with 80% ethanol (EtOH) (60°C, 20 min), centrifuged, and reextracted with 80% EtOH–diethyl ether (1:1 v/v, 60°C, 20 min). After centrifugation, the combined supernatants constituted the lipid fraction. Occasionally, "lipid" fractions were further separated into alcohol-soluble, ether-insoluble (protein) and alcohol-soluble, ether-soluble (lipid) components. More than 90% of the total label in the alcohol-soluble fraction was partitioned into the ether phase (lipid). Since ^{32}P was never significant in the ether-insoluble portion, this separation was not routinely performed.

After lipid extraction, the residue was dissolved in 1 *M* KOH and heated at 60°C for 1 h, after which the suspension was neutralized with 2 *M* HCl and made to 10% TCA. Following 20 min in ice, the sample was centrifuged and the pellet rinsed with 10% TCA. The combined supernatants contained the cellular RNA. No attempt was made to isolate polyphosphate fractions b and c during the KOH extraction (Cembella et al. 1984b). The final step involved dissolving the residue in 0.1 *M* NaOH and contained DNA, protein, and high molecular weight polyphosphate (PolyP d). Complications arising in the extraction of PolyP will be outlined in the discussion section.

Less than 0.5% of the total radioactivity resisted hot (90–100°C) acid hydrolysis (2 × 20 min) after the RNA extraction, indicating negligible ^{32}P labelling of protein. Whole fractions were counted in PCS (Amersham) for 20 min or 40 000 counts on a Searle Mark III liquid scintillation counter.

Results

Seasonal Patterns

Uptake of carrier-free $^{32}PO_4$ was generally slower during spring and fall compared with summer (Lean et al. 1987). Subcellular incorporation patterns for populations exhibiting slow PO_4 turnover are exemplified by the experiment conducted at the midlake station (403) on 20 October (Fig. 1). Despite low soluble reactive phosphate (SRP) of 1 $\mu g\ P \cdot L^{-1}$ and warm water (12.2°C), the turnover time was 12.9 h. Fifty percent of the added carrier-free $^{32}PO_4$ was filterable after 21 h, and when assayed with added PO_4 (33 $\mu g \cdot L^{-1}$) for the same period, uptake was reduced to 6%.

The distribution of the cellular ^{32}P as a percent of incorporated label provides additional information to that above (left panels, Fig. 2). The rapidity of P assimilation is emphasized by

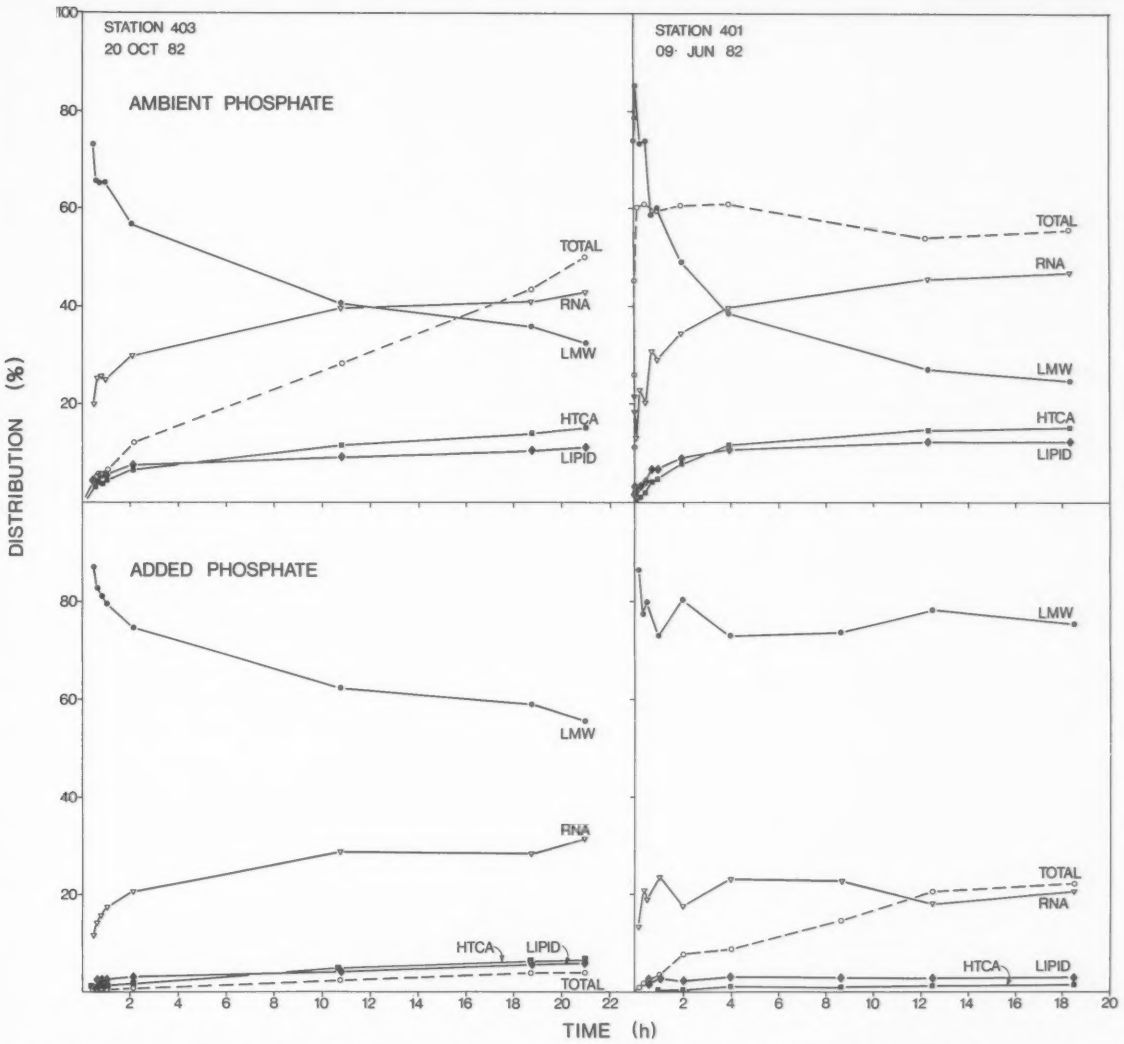

FIG. 2. Uptake of radioactive PO_4 (○) and subcellular distribution expressed as a percent in the particulate fraction for LMW (●), RNA (▽), lipid (◆), and HTCA (■) for samples collected at station 403 on 20 October 1982 (left panels) and station 401 on 9 June 1982 (right panels).

the fact that by the first sampling point (~10 s), more that 20% of the ^{32}P had already passed through the LMW compartment into macromolecules. As accumulation of exogenous ^{32}P into LMW slowed, the LMW pool lost radioactivity hyperbolically with time primarily to RNA. By the end of the experiment, RNA was the principal subcellular fraction (40%), while carrier-free isotope moved through LMW to RNA and to a lesser extent the HTCA and lipid fractions. With added P, LMW remained the principal form of assimilated P. The proportion in RNA, HTCA, and lipid fractions was lower. After 21 h, uptake was neither complete nor was a steady state of the subcellular fractions achieved in either case.

A contrasting regime is depicted by an experiment on 9 June along the north shore (station 401) where the thermal bar was present and the temperature had risen to 10.8°C even though the temperature at the midlake station was only 3.1°C. This experiment provides an example of rapid PO_4 turnover time (12 min). In fact, this was the most extreme P deficiency observed at the north shore station over the entire study period (Lean et al. 1987). Uptake of carrier-free PO_4 was complete in less than 1 h, but the isotope flow among subcellular compartments continued for more than 18 h (right panels, Fig. 2). The LMW fraction dropped progressively to 25% of the assimilated ^{32}P with a corresponding increase in RNA to 47%, HTCA to 15%, and lipid to 12%. In contrast, uptake of isotope in the P-enriched sample continued for more than 18 h but the subcellular fractions had reached a steady state within about 2 h. With added P, the LMW fraction also contained about 80% of the initial assimilated ^{32}P, but instead of declining, the LMW^{32}P remained near 75%. RNA increased from initial values near 15% to about 20%. The HTCA and lipid fractions stabilized within 4 h at 1.5 and 3%, respectively.

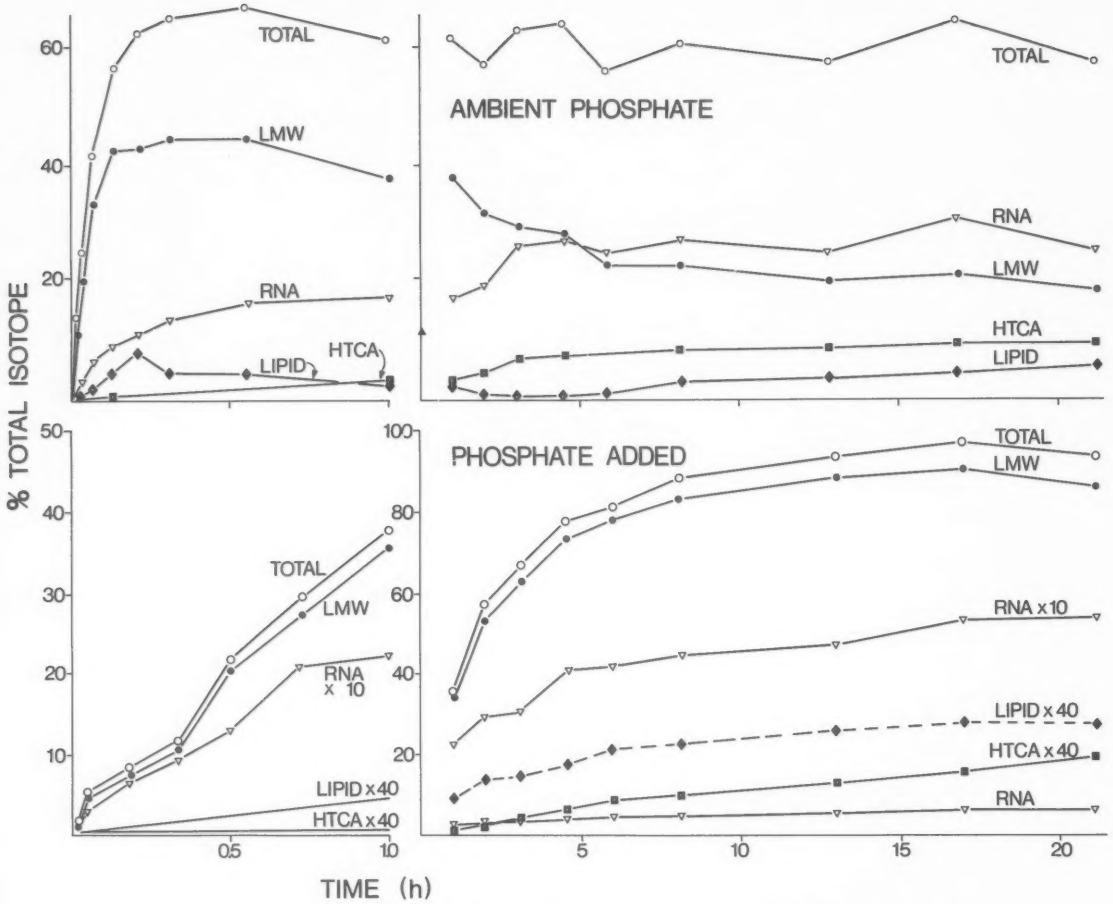

FIG. 3. Symbols as in Fig. 1. Changes over the first hour are shown on an expanded scale on the left.

The 9 June data are replotted (Fig. 3) as in Fig. 1 but are shown on an expanded scale over the first hour. The most significant feature is that the carrier-free ^{32}P remains in LMW form. Since there was little additional uptake during the next 19 h, the long equilibration times of the RNA and LMW compartments provide information on the exchange rates between these compartments. With added PO_4 (lower panels, Fig. 3), LMW continues to represent the predominant form and net uptake of PO_4 continues over the entire period. This represents a tremendous and rapid loading of P into labile LMW pools available for either storage (PolyP) or biosynthesis as needed.

With added PO_4, only 22% (i.e. 7 $\mu g\ P \cdot L^{-1}$) of the isotope was taken up, but this represents a doubling of the original particulate P concentration. Since LMW was being resupplied with radioactivity, it continued to increase (i.e. ^{32}P uptake and assimilation was greater than the rate of incorporation of LMW into RNA). The increase in RNA was about one quarter that for LMW and explains the constant distribution of about 20 and 80% for these two forms (Fig. 2). Our technique does not distinguish DNA from high molecular weight polyphosphate (see Discussion), so the increase in HTCA could be labelling of either of these forms. Low molecular weight polyphosphate is in the LMW fraction (see below).

Experiments conducted at Jacks Lake provided a higher degree of P deficiency, even though the levels of chlorophyll and P are similar to that in Lake Ontario. Turnover times are routinely less than 5 min (Lean et al. 1987). Incorporation of carrier-free ^{32}P into subcellular components followed a similar pattern to that for P-deficient populations in Lake Ontario. Furthermore, the response to added P was also similar qualitatively, but there was a much greater proportion of the assimilated ^{32}P in the LMW component. With a particulate P concentration of 7 $\mu g\ P \cdot L^{-1}$, the uptake velocity with added PO_4 of 10 $\mu g\ P \cdot L^{-1} \cdot h^{-1}$ over the first hour represents a biomass specific increase of greater than $1 \cdot h^{-1}$. By 22 h, almost all the added 33 $\mu g\ P \cdot L^{-1}$ was taken up, more than quadrupling P biomass, yet over 90% of this amount remained in the LMW fraction.

Pulse-chase experiments were conducted at different times during experiments such as those described above by additions of PO_4 (1 μM) to half of the carrier-free subsample. For example, the plankton at station 401 on 24 August were so P deficient that with added P (1 μM), particulate P increased

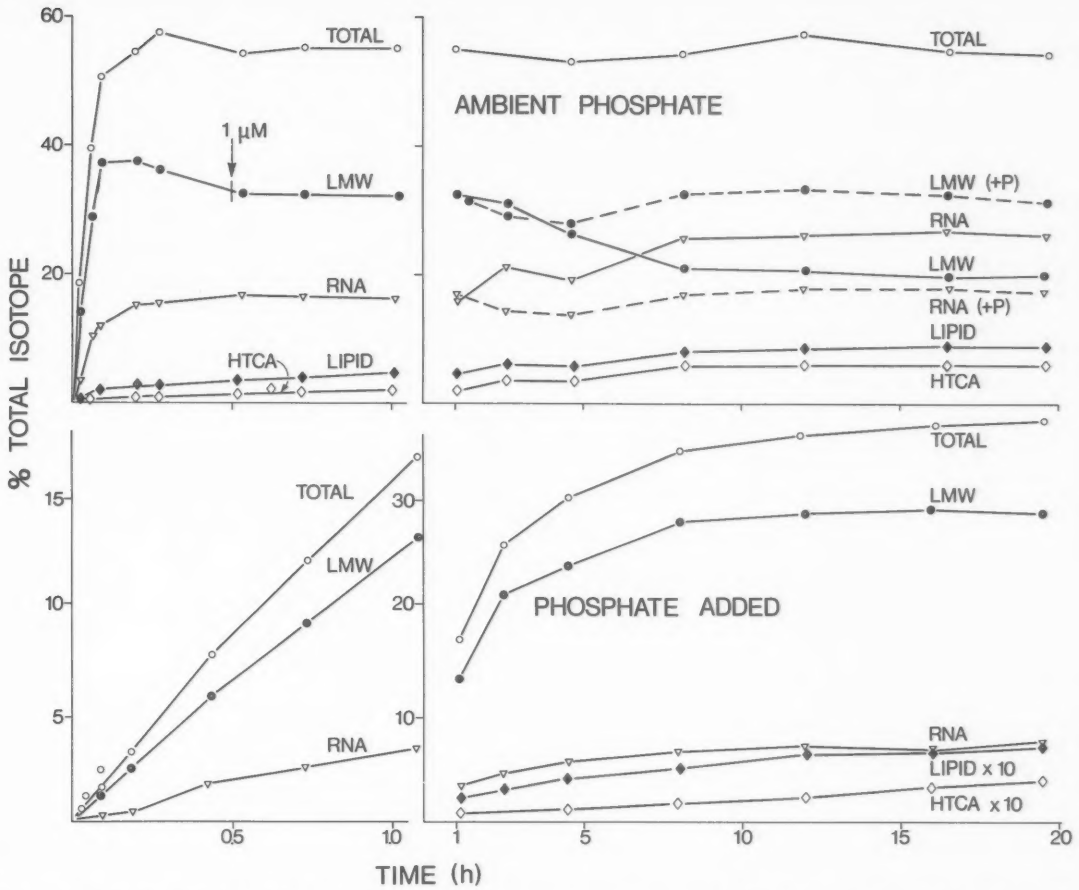

FIG. 4. Symbols as in Fig. 1. After 0.5 h the sample with carrier-free isotope was divided in half and 1 µ*M* PO_4 added. Changes in this chase experiment are shown with a broken line.

threefold in less than 30 h and doubled in just 30 min (Fig. 4). The uptake of carrier-free isotope was complete within 0.3 h, with LMW retaining about 80% of the initial label. Since the uptake of isotope was complete, this would have the effect of flooding the LMW compartment with cold PO_4. Instead of decreasing, LMW^{32}P remained constant (broken line, Fig. 4), indicating that LMW^{32}P was not exchanging with the medium. RNA^{32}P did not increase as much as in the control with no P chase, reflecting the lower specific activity of the LMW compartment. The lipid and HTCA fractions also failed to increase (not shown) as much as in the sample with no P chase. Perhaps equally significant, the recently acquired ^{32}P was not lost from RNA after the P chase. This suggests that a simple-compartment model with interconnecting exchange reactions does not apply, or is insignificant compared with the net uptake and assimilation processes which occur when PO_4 is added. Without the P chase, LMW^{32}P decreased with a corresponding increase in RNA. When P was added soon after uptake was complete, transfer to RNA was blocked. When added after the subcellular fractions had equilibrated, subsequent changes were not found. Even at higher levels of added P (20 µ*M*), radioactivity was not chased from the cells or from the rapidly "exchanging" compartments.

Data in Table 1 represent a wide range of rates for uptake and subcellular distribution. These differences could be caused by a combination of factors including temperature, biomass, different species, different plankton size distribution, and changes in the degree of P deficiency. In the carrier-free experiments, 37.2 ± 9.2% (n = 10) was in RNA. Temperatures did not seem to influence the subcellular distribution but may have increased the time to reach equilibrium. With added PO_4, RNA was 19.4 ± 6.0% (n = 8). Low percent as RNA values were found at station 403 on 25 August during the peak of chroococcoid cyanobacteria (Pick and Caron 1987). Since added PO_4 reduced the percent as RNA and increased the proportion in the LMW fraction, it would seem that a certain degree of P deficiency was present in all populations throughout the experimental period, but further refinement of LMW is required (see below).

P Uptake by Different Sizes of Microorganisms

The uptake of carrier-free ^{32}P appeared to stop at 60–70% in experiments where the turnover time of PO_4 was rapid (Fig. 3; Table 1). At such times, uptake is principally by bacteria and picoplankton (Lean et al. 1987). GF/F filters have a nominal pore size of 0.7 µm and retain most of the phytoplankton but not

TABLE 1. Time to reach uniform isotopic distribution between particulate and dissolved fractions (UPT) and subcellular fractions (SCF). Also shown with the steady-state subcellular distribution are corresponding temperature and chlorophyll *a* values. (+P) = with added PO_4; (−P) = without added PO_4. If equilibration was not reached, values (+/−) indicate further changes.

Date (exp.)	Temp. (°C)	Chl *a* ($\mu g \cdot L^{-1}$)	Time (h)		^{32}P distribution (%)			
			UPT	SCF	LMW	Lipid	RNA	HTCA
			Station 401					
7 Apr. (−P)	1.2	3.7	+20	+20	−58	3	+37	2
9 June (−P)	10.8	3.0	1	+18.4	−25	12	+47	16
9 June (+P)	10.8	3.0	+18.4	2	75	3	20	2
29 June (−P)	8.2	4.1	2	15	15	8	36	5
29 June (+P)	8.2	4.1	+20	2	80	3	15	2
24 Aug. (−P)	14.5	4.4	2	16	45	6.5	40	8.5
24 Aug. (+P)	14.5	4.4	+20	2	79	2	19	0.4
			Station 403					
10 June (−P)	3.1	2.5	+18	+18	−65	6	+28	0.4
15 July (−P)	15.7	6.7	1	—	32	10	42	16
15 July (+P)	15.7	6.7	—	—	71	2	26	1
12 Aug. (−P)	18.8	2.5	1	12	55	9	30	6
12 Aug. (+P)	18.8	2.5	+20	2	80	3	15	2
25 Aug. (−P)	16.6	4.6	1	10	79	2	18	1
25 Aug. (+P)	16.6	4.6	+20	3	87	1	12	−1
22 Sept. (−P)	16.5	6.6	2	20	40	10	42	8
22 Sept. (+P)	16.5	6.6	+20	2	76	4	18	2
20 Oct. (−P)	12.2	3.9	+21	+21	−32	+11	+42	+15
20 Oct. (+P)	12.2	3.9	+21	+21	−58	+6	+30	+6
			Jacks Lake					
17 Aug. (−P)	22.0	4.6	<1	20	32	8	44	16
17 Aug. (+P)	22.0	4.6	+20	2	94	1	5	0.4

all the bacteria. With added PO_4, uptake shifts to larger sized plankton and GF/F filters retain nearly as much isotope as the 0.2-μm Nuclepore filters (Table 2).

Since there was an observed shift in the size distribution of the organisms responsible for isotope uptake with added PO_4, changes in subcellular distribution could be due to either the size of the organisms responsible for uptake or the PO_4 enrichment itself.

To determine the influence of cell size on isotope distribution and to further describe components of the LMW compartment, the phosphomolybdate complex of the normal SRP assay (Strickland and Parsons 1972) was extracted with diethyl ether, isolating PO_4 from low molecular weight organic phosphorus (POP) and low molecular weight polyphosphate (PP). Two experiments were conducted in Lake Ontario near station 403 on 23 July and 18 September 1984, but the most extreme example of P deficiency was again found in Jacks Lake on 11 August. The subcellular distribution of such populations were compared with the same population with added PO_4 sufficient to shift a portion of the uptake to the larger plankton size classes. These results were compared with plankton samples that were prefractionated (<5 μm) pior to the PO_4 addition and from postfiltration (filter fractionated after isotope labelling). As previously noted (Table 1), the percent as RNA was much higher in the carrier-free experiments than for those with PO_4 added (Table 3). Samples prefiltered through 5-μm Nuclepore filters were similar to the whole-lake water samples showing that differences in distribution were not due to the size of the plankton responsible for the uptake of PO_4. The <5 μm fraction without added P exhibited features suggesting that PO_4 was released during the prefiltration procedure. The uptake was principally by this fraction (see below) in the WLW sample, but after prefiltration, uptake was slower. The percent uptake was more like that with added P, again suggesting that some P was released during prefiltration. The fraction containing low molecular weight polyphosphate and particulate organic phosphate (PP+POP) increased with added PO_4.

Postfiltration results are compared with the prefiltration values at 1.5 and 2.5 h of incubation (Table 4). The amount as cellular PO_4 appears to be slightly less with corresponding increases in PP+POP when larger cells are included, but the results are very similar in all examples. The differences observed in the distribution of label within the cells could not be due to shifts in the size distribution of plankton responsible for uptake. Values for turnover time of PO_4 for the Lake Ontario September experiment and the Jacks Lake experiment are shown in Table 5. Approximately 69 and 58% of carrier-free uptake was due to the 0.2–1.0 μm fraction in the Jacks Lake and Lake Ontario examples, respectively. This shifted to only 3.5 and 5.9% with added P. The >12 μm fraction was only 4.7% of the carrier-free uptake for the Jacks Lake sample but increased to 44% with added P. The >12 μm fraction uptake for the Lake Ontario sample also increased from 1.1 to 22.4% with added P. The efficiency of retention of activity of GF/F filters followed a similar pattern as in Table 2, increasing from 64 to 96% of the uptake measured using 0.2-μm filters with added PO_4.

Results from 18 September are presented to illustrate the patterns of labelling of the subcellular fractions. Figure 5 shows

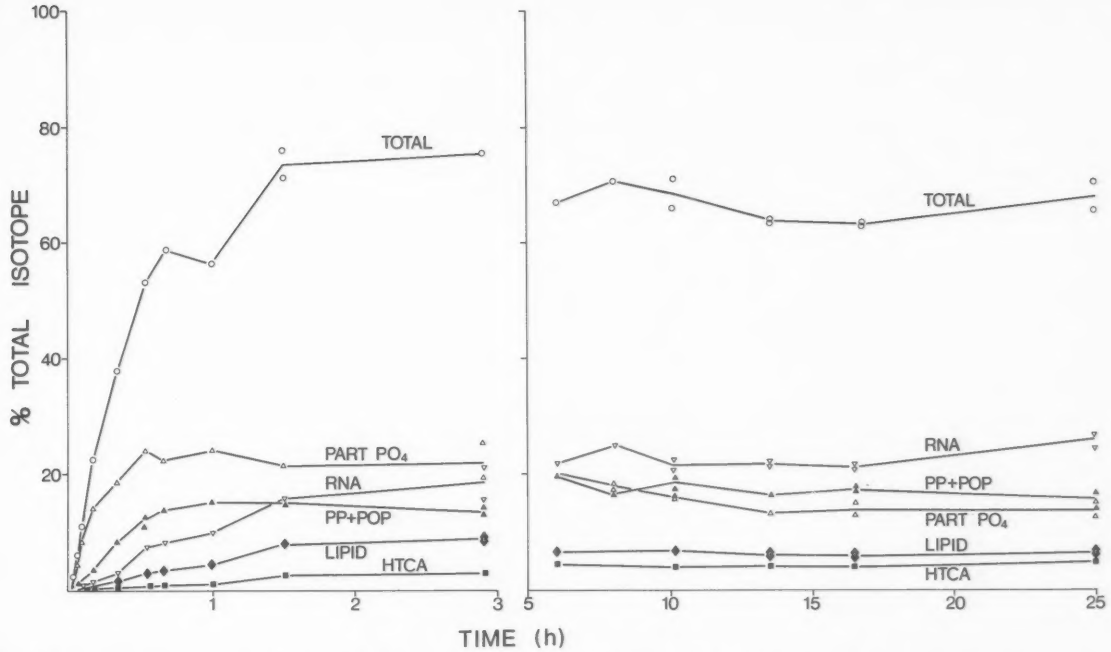

FIG. 5. Isotope uptake expressed as a percent of total activity (○) and in particulate PO_4 (△), low molecular weight polyphosphate plus particulate organic phosphate (▲), RNA (▽), lipid (◆), and HTCA (■) as a function of incubation time. Experiments were conducted at a station near 403 on 18 September 1984 at ambient PO_4 concentrations. Changes over the first hour are shown on an expanded scale on the left.

TABLE 2. Percent uptake of carrier-free radioactive PO_4 with (+P) and without (−P) added PO_4 by different-sized Nuclepore filters compared with Whatman GF/F glass fibre filters. The incubation time (IT) refers to the time when the comparison was made. Also shown is the PO_4 turnover time (PTT).

Date (exp.)	PTT (h)	IT (h)	% uptake GF/F	0.2	1.0	5.0	12
Station 401							
7 Apr. (−P)	67	18	—	1.2	0.8	0.4	0.2
9 June (−P)	0.21	2.6	60.5	84.7	28.3	6.5	5.5
9 June (+P)	52	6.5	12.5	13.5	12.8	5.8	4.7
29 June (−P)	0.6	0.9	61.0	66.0	19.9	5.9	4.6
29 June (+P)	26.1	1.2	4.8	4.6	3.8	2.3	1.7
24 Aug. (−P)	0.1	1.0	54.5	93.8	35.8	3.1	0.6
24 Aug. (+P)	10.9	1.2	20.0	21.6	18.8	2.6	1.0
Station 403							
15 July (−P)	0.15	1.5	56.0	99	34.3	5.6	2.1
15 July (+P)	12.9	2.0	10.6	12.5	10.6	4.2	1.4
12 Aug. (−P)	0.2	1.3	64.2	93.4	58.4	5.2	1.7
12 Aug. (+P)	15.8	1.5	8.0	8.3	7.3	2.1	0.4
25 Aug. (−P)	0.3	1.5	67.7	95.6	52.2	1.5	0.7
25 Aug. (+P)	23.3	1.6	6.6	7.4	6.2	1.1	0.3
22 Sept. (−P)	0.7	1.1	54.5	67.7	21.8	4.6	2.9
22 Sept. (+P)	28.4	1.3	4.5	4.5	3.9	2.7	1.5
20 Oct. (−P)	12.9	1.5	10.0	13.3	5.5	2.3	1.8
20 Oct. (+P)	112	2.0	1.7	1.8	1.5	0.9	0.7
Jacks Lake							
17 Aug. (−P)	0.08	1.5	64.3	96.8	29.6	11.0	4.8
17 Aug. (+P)	4.0	0.75	27.6	43.3	31.3	20.7	11.9

the pattern for carrier-free uptake of isotope for WLW. Initial uptake was principally as PO_4 (recall LMW = PO_4 + PP+POP) with PP+POP increasing more slowly. RNA, lipid, and HTCA follow. By 8 h, the distribution (Table 3) was maintained with PP+POP equal to about 25% of the total uptake.

With added PO_4 (0.6 *M*) about 8% of the added isotope was taken up in 2 h (Fig. 6), but by 23 h, this had increased to 24%. During the initial rapid uptake phase, PP+POP increased from about 20 to 44%. For the remaining period, all fractions increased at a proportional rate, making the subcellular distribution appear constant. The prefiltered fraction <5 μm shows a similar pattern (Fig. 7) to that for whole-lake water except that the capacity to assimilate PO_4 was less. This may have been due in part to the lower biomass, but smaller cells may not be as P deficient as larger cells (Lean et al. 1987). Nevertheless, the labelling pattern is similar to that for WLW. This supports the view that differences observed in the distribution of isotope (Tables 1 and 3) were due to the deficiency of the cells rather than shifts from small to larger plankton with added PO_4.

Discussion

In Lake Ontario, the subcellular distribution of radioactive PO_4 followed a consistent pattern from April to October 1982. RNA ^{32}P values were near 40% in carrier-free experiments but declined to near 20% with added PO_4. With added P a corresponding increase in LMW ^{32}P resulted from storage of LMW PolyP. Since there was no net increase in cellular PO_4 in the carrier-free experiments, ^{32}P was simply equilibrating with the metabolically active particulate fractions.

While subcellular transformations occurred rapidly, PO_4

TABLE 3. Time to reach uniform isotopic distribution for uptake UPT) and subcellular fractions (SCF) for whole-lake water (WLW) and through 5 μm with (+P) and without (−P) added PO_4. At isotopic equilibration the isotopic distribution within the particulate fraction is provided. LMW was subdivided into cellular PO_4 and polyphosphate plus low molecular weight particulate organic phosphate (PP+POP).

Date, sample (exp.)	Time (h)		^{32}P distribution (%)				
	UPT	SCF	PO_4	PP+POP	Lipid	RNA	HTCA
Lake Ontario							
23 July							
WLW (−P)	15	15	32	20	8	35	5
WLW (+P, 0.2 μ*M*)	+24	10	20	55	2	18	5
<0.5 μm (−P)	15	10	15	48	4	30	3
<0.5 μm (+P, 0.2 μ*M*)	+24	+24	31	−45	2	+20	2
18 Sept.							
WLW (−P)	1.5	8	25	25	9	35	+6
WLW (+P, 0.6 μ*M*)	+30	12	32	44	6	16	+2
<0.5 μm (−P)	4	12	42	18	6	29	+5
<0.5 μm (+P, 0.6 μ*M*)	+30	12	27	45	6	20	+2
Jacks Lake							
11 Aug.							
WLW (−P)	0.3	4	23	14	13	44	+6
WLP (+P, 0.6 μ*M*)	+23	2	31	52	3	14	0.3
<0.5 μm (−P)	0.5	2	31	29	8	30	+2
<0.5 μm (+P, 0.6 μ*M*)	+23	2	45	38	3	13	0.6

TABLE 4. Subcellular distribution of radioactive PO_4 plus added PO_4 (0.6 *M*) for experiments conducted on 18 September for prefiltered (PRE) and postfiltered (POST) samples. WLW = whole-lake water.

Samples	Time (h)	Filter size (μm)	Subcellular distribution (%)				
			PO_4	PP+POP	Lipid	RNA	HTCA
POST	1.5	1	47.2	26.5	5.4	18.9	2.0
POST	1.5	3	45.7	34.4	4.4	14.5	1.0
POST	1.5	5	44.1	40.0	3.3	11.9	0.7
POST	1.5	12	44.2	38.5	4.3	12.3	0.6
WLW	1.5		50.0	35.0	3.5	10.9	0.6
PRE	1.5	5	39.5	39.0	4.5	16.0	1.0
POST	2.5	1	44.5	31.4	5.0	17.4	1.7
POST	2.5	3	44.3	37.5	4.2	13.0	0.9
POST	2.5	12	40.7	45.9	3.2	9.6	0.6
WLW	2.5		43.4	40.0	4.0	12.0	0.6
PRE	2.5	5	30.8	45.5	4.5	18.0	1.2

TABLE 5. Percent uptake of carrier-free radioactive PO_4 at ambient (amb.) and PO_4-enriched (+P) concentrations by different-sized Nuclepore filters compared with Whatman GF/F glass fibre filters. The incubation time (IT) refers to the time when the comparison was made. Also shown is the PO_4 turnover time (PTT). Values for isotope uptake are expressed as a percent of that retained on 0.2-μm Nuclepore filters.

Date (exp.)	PTT (h)	IT (h)	% uptake				
			GF/F	0.2	1.0	5.0	12
Jacks Lake							
11 Aug. (amb.)	0.1	19	62	100	30.7	8.5	4.7
11 Aug. (+P)	3.0	19	97	100	96.5	53.3	44.0
Lake Ontario							
18 Sept. (amb.)	0.75	2.5	66	100	41.9	5.5	1.1
18 Sept. (+P)	15.3	2.5	95	100	94.1	38.4	22.4

dominated the subcellular distribution during the first few minutes. As cellular $^{32}PO_4$ decreased, RNA and the fraction which includes PP+POP increased. In most cells, low molecular weight phosphate esters (POP) represent about 20% of the total particulate P (Bieleski 1973). This would imply that little LMW PolyP was formed. Although uptake of carrier-free isotope was complete within 1–3 h, subcellular distribution changed for periods of up to 16 h until the near-steady-state distribution shown in Fig. 8 was reached.

With the addition of PO_4, isotope uptake represents net increase in cellular P. Here the rate was more rapid over the initial 1- to 3-h period as the subcellular distribution shifted from that shown in Fig. 8 to that in Fig. 9. No longer was exchange between the particulate and soluble PO_4 pools significant. Although uptake continued for long periods (>20 h), within a few hours, all fractions increased at the same rate. If we assume that POP remained as only 20% of the total, then LMW PolyP increased until it represented 30% of the recently incorporated PO_4.

Independent estimates of polymeric P storage products were measured using the selective action of 253-nm UV light against organic P esters followed by acid hydrolysis for PolyP. The incorporation of ^{32}P into LMW Poly P or PolyP a as measured above was equivalent to values in total PolyP from this method. This means that little PolyP exists in the RNA or HTCA fraction.

Reviews of existing literature (Harold 1966; Kuhl 1974; Cembella et al. 1984b) suggest that "luxury" PO_4 uptake is principally directed to HMW PolyP. This includes PolyP b and c

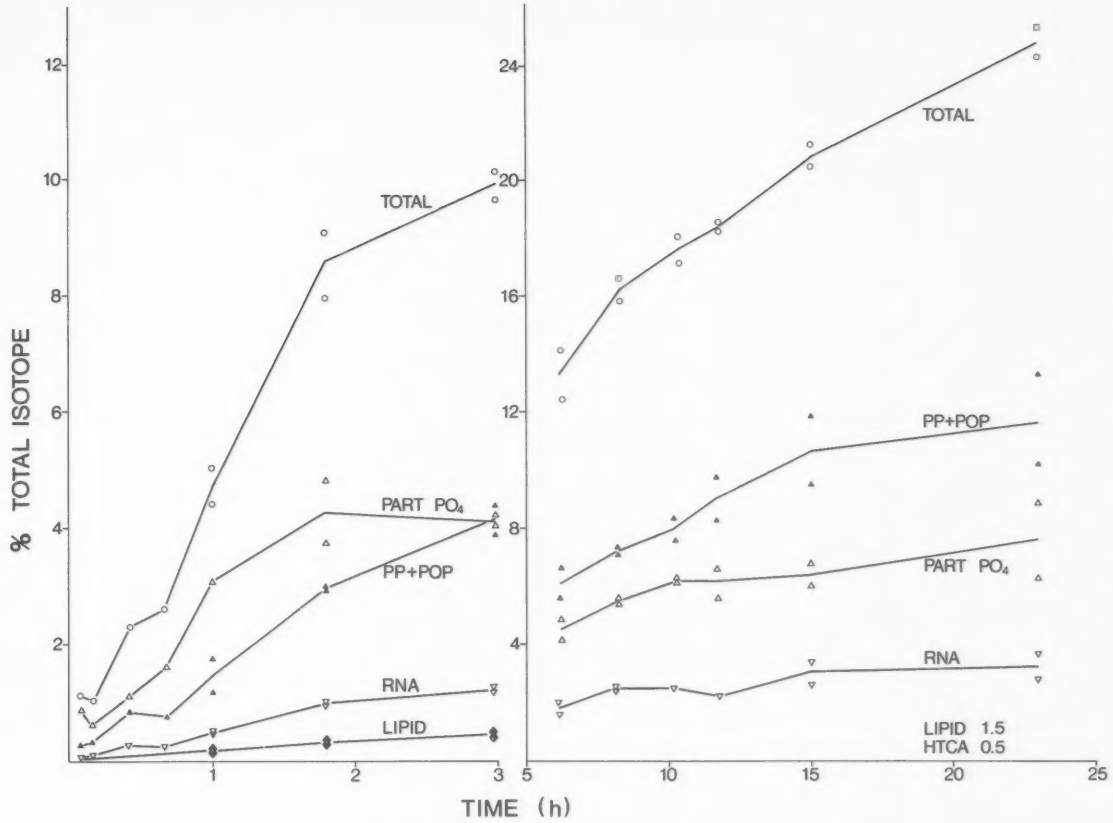

FIG. 6. Symbols as in Fig. 5 but at PO_4-enriched (0.6 μM) concentrations.

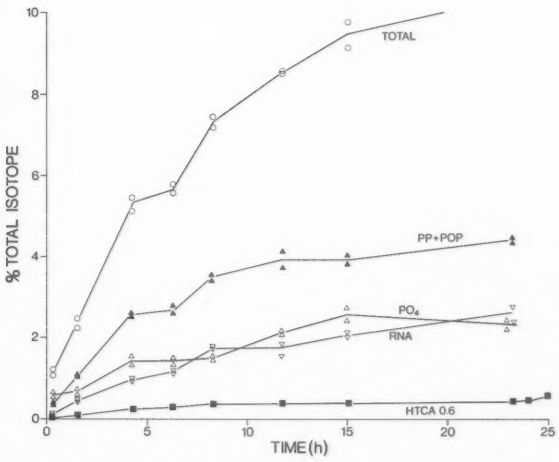

FIG. 7. Symbols as in Fig. 5 but for the <5 μm fraction only.

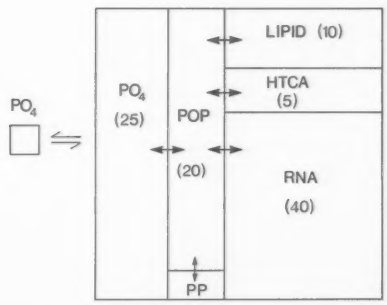

FIG. 8. Steady-state box model representing exchange between soluble PO_4 and cellular PO_4. Other subcellular fractions are shown in proportion to equilibrated isotope distribution.

in our RNA fraction and PolyP d in the HTCA fraction. In our experiments, HTCA was not a predominant subcellular fraction in any of the experiments with or without added PO_4. Arguing against PolyP b and c being important was the fact that the "RNA" fraction was lower in the PO_4-enriched samples. Instead, LMW, representing PO_4, LMW organic P compounds, and LMW PolyP were the principal fractions (Table 1).

Beever and Burns (1980) considered that PolyP with less than 20 Pi units would be soluble in TCA, while those with greater than 20 Pi units would be insoluble in TCA but noted Harold's (1966) contention that all forms of PolyP should be acid soluble regardless of chain length. Because polyphosphates are strong polyanions and bear negative charges even at acid pH, they

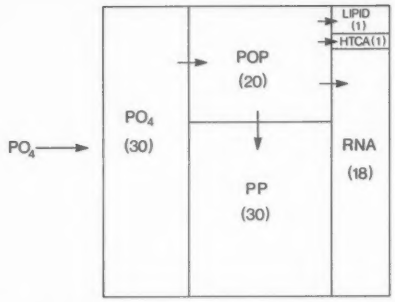

FIG. 9. Distribution of radioactive P in the particulate fraction during uptake under P-enriched conditions. Areas are in proportion to isotopic distribution.

combine with, and precipitate, positively charged macromolecules, such as proteins. The amounts of "soluble" and "insoluble" PolyP will therefore depend also on the availability of the basic receptor. Thus, the formation of acid-insoluble PolyP is probably an analytical artifact. In our experiments, 10 mL of Lake Ontario water gave sufficient radioactivity for the subcellular fractionation. For chemical analysis, over 500 mL would be required. This would concentrate proteins (and possibly metals) that would contribute to the formation of "acid-insoluble" PolyP. PolyP b and c may have been included in our RNA fraction, but since values from UV oxidation and acid hydrolysis for total PolyP were near our values for LMW PolyP, the quantity of PolyP b and c must be low. As Cembella et al. (1984b) pointed out, Hooper (1973) may have been correct in his assertion that binding of polyphosphate fractions to protein–RNA complexes represents an artifact of extraction. The first step in Kuhl's (1974) extraction involved an ether extraction for lipids. Without the cold TCA treament, many enzymes remain active. This may also have contributed to the discrepancy.

The subcellular distributions noted above apply irrespective of the plankton size class responsible for the uptake. Uptake from soluble phosphate esters cannot be determined, but added esters reduced the uptake of carrier-free PO_4 and shifted the subcellular distribution toward that found in enriched samples. This reaffirms the potential of phosphate esters to supplement planktonic P requirements (Cembella et al. 1984b; Pick 1987) if present in useful quantities.

Our subcellular fractionation experiments showed that the plankton were always P deficient to some extent. Larger algae dominate during turbulent conditions such as that found in spring and fall. Their higher half-saturation constants prevent them from depleting the PO_4 to the same extent (Lean et al. 1987). Consequently, rapid PO_4 turnover times are found only in the stratified periods. Under conditions of balanced growth, the subcellular distribution of label would be the same for experiments both with and without added PO_4. This was never found during the entire period of investigation in Lake Ontario.

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Interpretations of Alkaline Phosphatase Activity in Lake Ontario

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Pick, F. R. 1987. Interpretations of alkaline phosphatase activity in Lake Ontario. Can. J. Fish. Aquat. Sci. 44: 2087–2094.

Alkaline phosphatase activity (APA) in Lake Ontario reached maximum levels of 0.25 μ*M*P released·h^{-1} during 1982. Relatively high values were first detected in nearshore surface water in May concurrent with thermal bar development and at a later date (end of June) at a midlake station following transport of nearshore water to the middle. APA remained detectable throughout the summer but declined in mid-August as a result of upwelling events. With fall mixing, APA persisted throughout the entire water column. Additions of phosphate did not inhibit APA until enrichments were much greater than maximum ambient concentrations of soluble reactive P. The findings suggest that APA is not a sensitive indicator of P deficiency. APA activity was correlated with nanoplankton (2–20 μm) plus picoplankton (0.2–2 μm) biomass but not with total algal biomass. APA associated with particles greater than 12 μm was relatively unimportant.

L'activité de la phosphatase alcaline (APA) dans le lac Ontario a culminé é 0,25 μ*M* de P libéré par heure durant 1982. Des valeurs relativement élevées ont d'abord été détectées dans les eaux de surface près de la rive en mai, au moment de la formation de la thermocline et plus tard (à la fin de juin) dans un station située au milieu du lac par suite de la migration d'eaux de la rive vers cet endroit. L'APA est demeurée détectable durant tout l'été mais a diminué à la mi-août à cause d'une remontée des eaux. Lors de la mixtion automnale, l'APA s'est maintenue dans toute la colonne d'eau. Des ajouts de phosphate n'ont pas inhibé l'APA jusqu'à ce qu'ils fussent bien supérieurs aux concentrations maximales ambiantes de P réactif soluble. Les résultats suggèrent que l'APA n'est pas un bon indicateur d'une déficience en P. L'APA a été corrélée avec la biomasse du nanoplancton (2–20 μm) et du picoplancton (0,2–2 μm) mais non avec la biomasse totale des algues. L'APA associée à des particules supérieures à 12 μm était relativement faible.

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Elevated phosphatase activity in aquatic systems is generally thought to indicate conditions of P deficiency (Fitzgerald and Nelson 1966; Perry 1972; Jones 1972a, 1972b; Healey 1973). Phosphatases can make available to microorganisms a fraction of the dissolved organic P pool by hydrolyzing phosphate ester bonds and releasing orthophosphate(P_i) for direct uptake, thus serving a potentially important role in the recycling of P in the euphotic zone. However, the size of the organic P pool that can be broken down by phosphatases is not known. Although techniques are available to measure phosphatase activity (Fitzgerald and Nelson 1966; Hill et al. 1968; Perry 1972), the importance of this mechanism compared with other means of P regeneration, such as zooplankton excretion, has not been clearly established.

The object of this study was to estimate the magnitude of phosphatase activity over a season in Lake Ontario and evaluate its potential as an indicator of P deficiency of the plankton. If phosphatase is to be used as an index of P deficiency, it should reflect rapid changes in cell nutrient status that accompany sudden inputs of nutrients. Information on cell nutrient status over the season can be found in Lean et al. (1987). In addition the distribution of phosphatase activity between particulate seston size classes and a "dissolved" fraction (below 0.2 μm) was measured so that the organisms responsible for the observed activity could be identified. These data were compared with phosphatase measurements from Jacks Lake, a small lake of similar trophic state where other indicators of nutrient deficiency have been measured (Pick et al. 1984a, 1984b).

Materials and Methods

Water samples were collected with Niskin bottles from the CSS *Limnos* at stations 401, 403, and 405 (Lean 1987) on nine cruises through 1982.

The fluorometric method of Hill et al. (1968), which provides more sensitivity than spectrophotometric methods (Pettersson and Jansson 1978), was used with some of the modifications of Healey and Hendzel (1979) to quantify alkaline phophatase activity (APA). A Turner 110 fluorometer was equipped with a Wratten 47B primary filter and a 2A 12 secondary filter with the window set at 1×. The substrate, 3-methylfluorescein phosphate (MFP) (Sigma), was made up in 10 m*M* Tris buffer (pH 8.5) and added at a final concentration of 1 μ*M* (0.05 mL of a 100-μ*M* stock to 4.5 mL of sample). In Lake Ontario, this level was found to be sufficient to obtain saturation kinetics and not cause substrate limitation during the assay. The time course of methylfluorescein production (i.e. phosphate release) was linear over 2 h, and measurements were taken at time 0 and

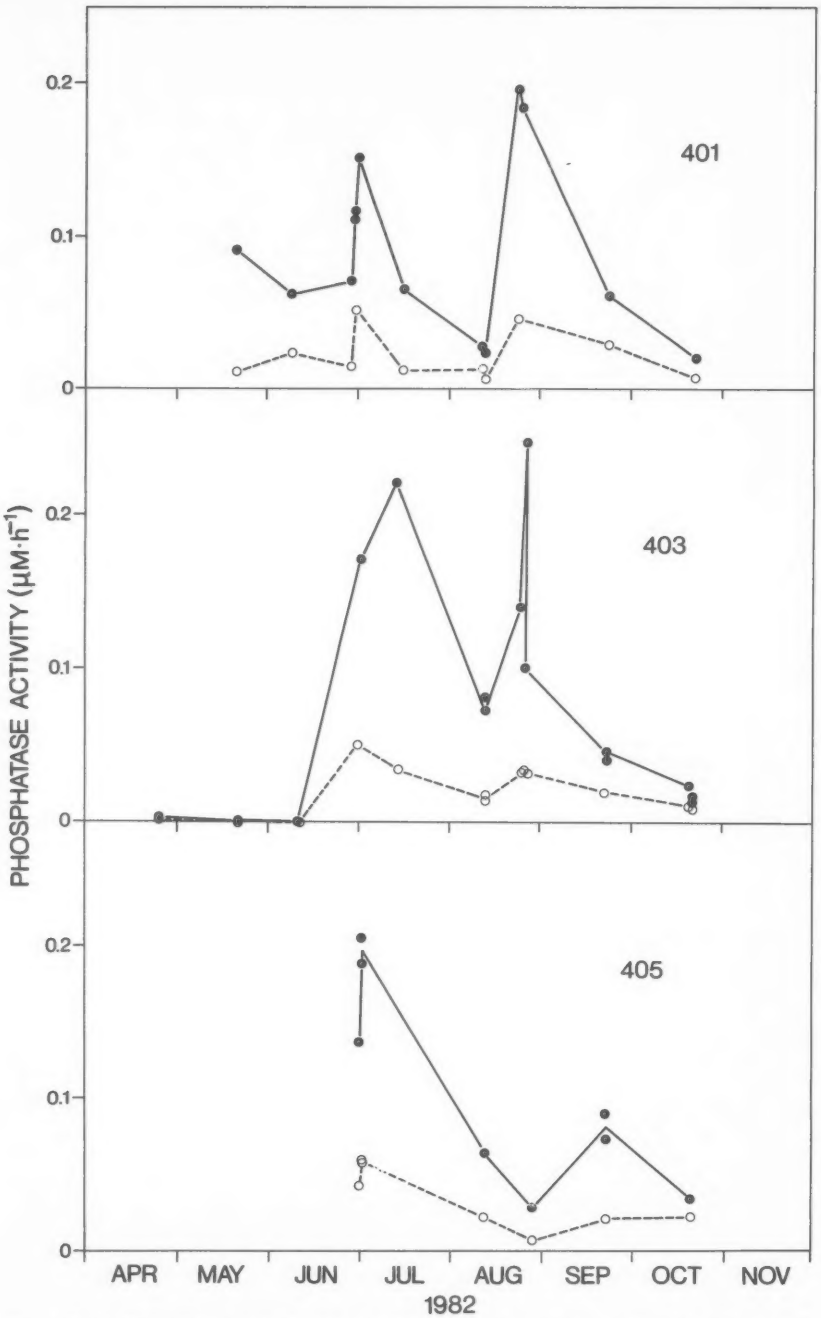

FIG. 1. Total (●) and "dissolved" (○) APA (μM MFP·h^{-1}) of Lake Ontario epilimnetic water (5 M) at stations 401, 403, and 405 in 1982.

intervals thereafter so that at least six points were taken over the first hour for each assay (the mean correlation coefficient for the release of methylfluorescein over time was 0.99 for 250 assays). Triplicate samples were periodically run, but replication is good with this method (less than 3% variation). The pH of Lake Ontario is 8.0–8.7, and this level was maintained in the assay without the addition of buffer so that APA was being measured. Duplicate 4.5-mL samples of whole lake water (WLW) and duplicate samples of 0.2-μm-filtered (Nuclepore) lake water (FLW) were incubated at 35°C, which gives maximum phos-

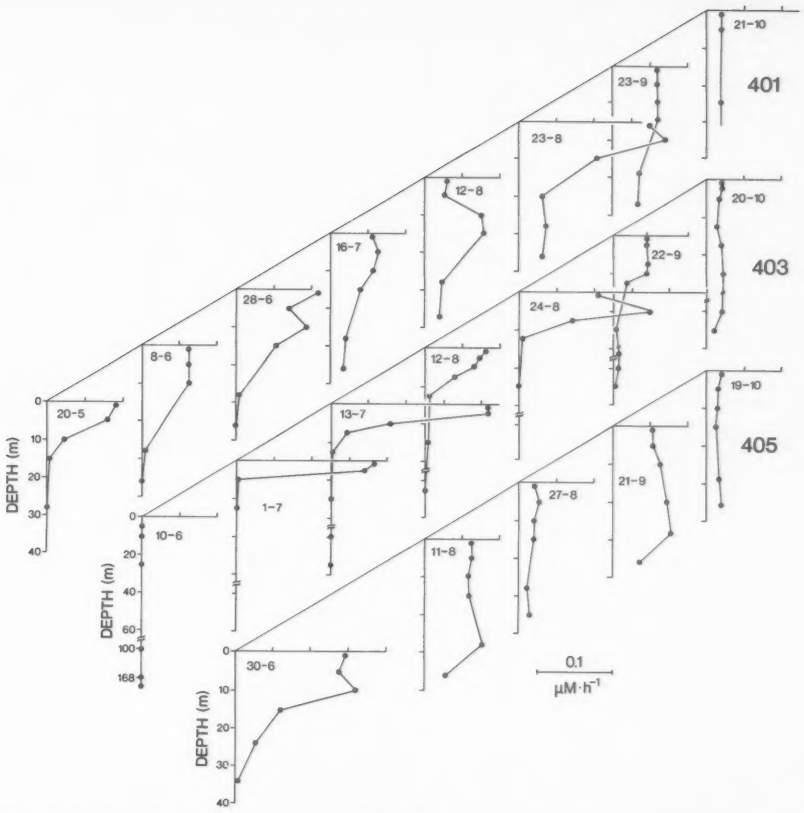

FIG. 2. Depth profiles of total APA (μM MFP·h^{-1}) at stations 401, 403, and 405. Sampling dates (day–month) are shown in each graph.

phatase activity. Sterilized distilled water served as a control. The effect of temperature on enzyme activity was examined on several dates throughout the season.

The inhibition of APA by additions of P_i and the effects of various organic P compounds on enzyme activity were examined. The APA of size fractions of the plankton was measured on lake water filtered through 12-, 5-, and 1-μm Nuclepore filters. Filtration vacuum pressure was kept at 14 kPa. Water chemistry and chlorophyll *a* measurements were made by the Water Quality Branch of the Canada Centre for Inland Waters (Environment Canada 1979). Information on phytoplankton biomass and nanoplankton biomass was obtained from Gray (1987) and Pick and Caron (1987), respectively.

Results

Enzyme activity was first detected inshore at station 401 in May in the surface waters (Fig. 1) when the thermal bar was present and the water temperature was 9°C. Water from 5 m was representative of the epilimnion and usually gave the highest value with depth (Fig. 2). APA was not detected offshore (station 403) until July. Two major seasonal peaks of activity were recorded at all three stations (Fig. 1). At 401 the first peak was found in the beginning of July and the second during the third week of August. At 403 the first peak was shifted to the middle of July and the second peak was measured over 3 d in late August. Measurements were not as complete for 405 but it too shows two peaks, the first one in the first week of July as for 401 but the second in the third week of September rather than August. Periods of depressed activity were recorded at all three stations towards the middle of August.

"Dissolved" phosphatase activity measured on 0.2-μm FLW was significant in Lake Ontario at all stations (Fig. 1) and might still serve to generate P in the epilimnion. Over 50% of the total activity was in the filtrate in September and October as opposed to 15% in May at 401. When all epilimnetic measurements were analyzed, there was a positive correlation between WLW and FLW APA values ($n = 97$, $r = 0.77$, $p < 0.001$) over the season.

Depth profiles of APA at all three stations indicated that the activity was largely restricted to the epilimnion early in the year, but by mid-August, significant values were found below the thermocline to above the sediments at 401 and 405 and down to 60 m at 403 (Fig. 2) (mixing depths given in Simons and Schertzer 1987). By fall, APA was found at all depths sampled, even at the midlake station (178 m).

Varying amounts of APA occurred in the different size fractions of the plankton over the season at the three stations (Table 1). On most dates, there were two main peaks of activity: one at <0.2 μm (20–51% of the total activity) and the second at 1–5μm (13–62%), with the smallest amount of activity at >12 μm. Data from Jacks Lake are included and also indicate that

TABLE 1. Percent distribution of total APA in various size fractions.

Date	APA ($\mu M \cdot h^{-1}$)	Size distribution (%) <0.2 μm	0.2–1 μm	1–5 μm	>12 μm
Station 403					
12 Aug.	0.081	21	27	42	10
25 Aug.	0.093	30	1	62	7
22 Sept.	0.039	51	18	13	18
20 Oct.	0.013	48	28	24	0
Station 401					
29 June	0.111	35	10	15	40
13 June	0.022	41	14	19	26
Station 405					
1 July	0.204	28	10	50	12
21 Sept.	0.089	24	14	36	26
Jacks Lake					
17 Aug.	0.147	20	46	14	20

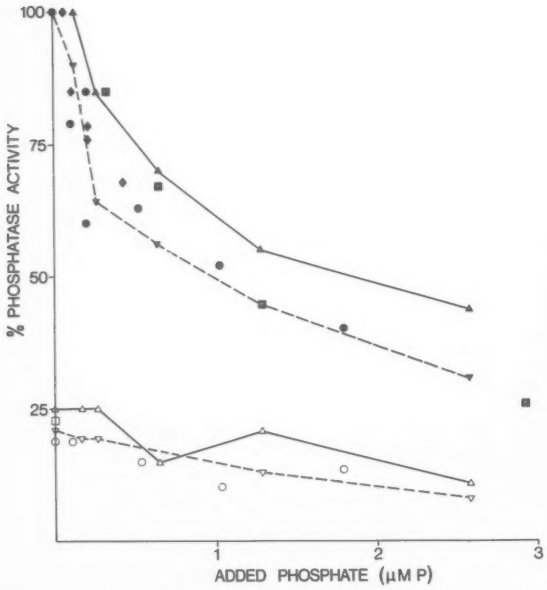

FIG. 3. APA shown as a function of added phosphate (expressed as a percent of the total APA at 0 added). Solid symbols represent total APA and open symbols the "dissolved" fraction of the total. Station 401 on 28 June immediately after inorganic P additions (■) and on 29 June after 30-h exposure (◆); station 403 on 12 August after 3-h exposure (●) and 25 August after 3- (△) and 18-h (△) exposures.

most of the APA is associated with plankton smaller than 12 μm in diameter.

Phosphate acts as a competitive inhibitor of APA, and the levels necessary to inhibit the enzyme are shown in Fig. 3. For 50% inhibition to occur, 1–1.3 μM P_i additions were required even when these high external P_i levels were maintained for 18 h (example of 25 August, 403). These concentrations were never measured in the lake where maximum concentrations of 0.2 μM for soluble reactive phosphorus (SRP) were measured only in April during 1982. Figure 3 also shows that the "dissolved" APA activity was suppressible to the same extent as APA associated with seston.

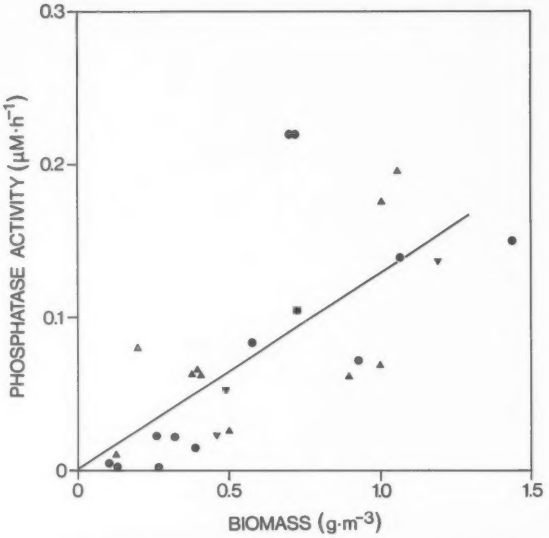

FIG. 4. APA in relation to corresponding concentrations of nanoplankton plus picoplankton biomass ($y = 0.002 + 0.127x$, $r = 0.69$, $p < 0.001$), stations 401 (▲), 403 (●), and 405 (▼).

When regression analyses were performed against ambient SRP, the negative correlation one would expect to find with APA was not significant even when APA associated with seston and normalized for biomass (chlorophyll *a*) was used. No single water chemistry parameter (namely total phosphorus (TP) and total filtered phosphorus (TPF) which would include the dissolved organic phosphorus (DOP) available for enzymatic hydrolysis) correlated significantly with APA measurements. Enzyme activity was not correlated with total algal biomass as estimated by inverted microscope techniques (Gray 1987), but a significant correlation ($r = 0.69$, $p < 0.001$) was found (Fig. 4) with nanoplankton and picoplankton (all microbes <20 μm) biomass estimated by epifluorescence (Pick and Caron 1987). Peaks of APA over the season (Fig. 1) corresponded with the peaks in picoplankton and nanoplankton numbers and biomass (Pick and Caron 1987, Fig. 1, 3). Although bacterial biomass alone did not correlate with APA, when it was included with the photosynthetic biomass <20 μm the relationship was improved over the relationship with photosynthetic biomass alone.

Substrate additions of 1 μM MFP were sufficient to saturate enzyme activity in Lake Ontario as shown in Fig. 5 where kinetic data from August 26 at 403 are shown. This date corresponded to the highest APA measurement obtained in Lake Ontario in 1982. K_t (substrate concentration supporting half the maximum APA) + S_n (natural substrate concentration) for this date was approximately 0.3 μM. When the V_{max} was lower, the $K_t + S_n$ was higher (405, 21 September $V_{max} = 0.13$, $K_t + S_n = 0.54$ μM. Maximum concentrations of natural substrates reacting in a similar manner to MFP are low when compared with the DOP pool measured chemically (range 0.12–2.5 μM in 1982).

Additions of glycerophosphate or pyrophosphate to the assay mixture resulted in reduced levels of APA,indicating that these phosphate esters were being hydrolyzed in a similar manner to

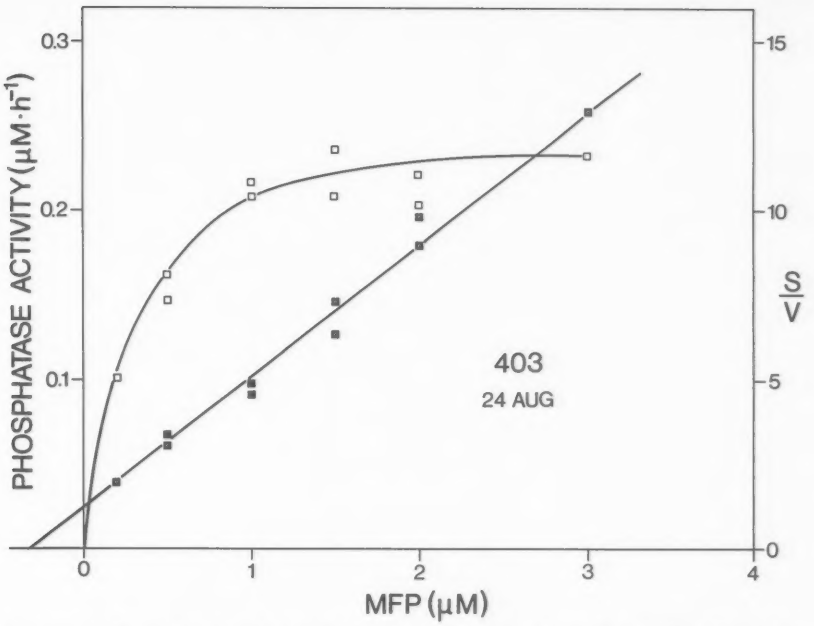

FIG. 5. APA (□) as a function of substrate additions of MFP and reciprocal plot of MFP addition/APA versus MFP (■), station 403, 26 August 1982.

TABLE 2. Influence of glycerophosphate or pyrophosphate addtions on APA ($\mu M \cdot h^{-1}$) measured with MFP (1 μM).

		Added substrate (μM)		
	Control	2	4	10
Station 401, 30 June				
Glycerophosphate	0.158	0.077	—	0.019
Pyrophosphate	0.158	0.048	—	0.02
Station 405, 1 July				
Glycerophosphate	0.205	0.075	0.055	0.026
Pyrophosphate	0.205	0.091	0.070	0.055

MFP (Table 2). If one assumes that at 1 μM MFP, V_{max} is reached, then glycerophosphate or pyrophosphate additions of 2, 4, and 10 μM should reduce the velocity of the reaction to 1/3, 1/5, and 1/11, respectively. Also, if some DOP was also reacting, an addition of 2 μM glycerophosphate would in fact reduce the velocity to less than 1/3. Velocity values thus calculated are all higher (for glycerophosphate, 1 July; 0.225, 0.275, and 0.286, respectively, compared with 0.205) than the assumed V_{max}, suggesting that these organic P esters were not equally preferred substrates.

The temperature dependence of APA was examined on several dates and the optimum was always achieved at 35°C, the temperature at which the assay was normally conducted. The Q_{10} for the reaction was 1.4 ± 0.08.

Discussion

APA values given here represent maximum values under optimum conditions of temperature and substrate sufficiency and thus reflect potential rather than real in situ rates. Values for Lake Ontario (and Jacks Lake) fall within those obtained in mesotrophic lakes and are similar to rates found in Lake Erken, Sweden, and Lake 239 of the Experimental Lakes Area of northwestern Ontario, when normalized to the same assay temperature (Table 3). Unfortunately, direct comparisons with literature values are not always possible, since there is a range of techniques employed even when the fluorogenic substrate MFP is utilized. Some workers choose to subtract "dissolved" APA from the WLW measurement because the latter does not represent APA associated with microorganisms (Healey and Hendzel 1979). Culture work has clearly shown the importance of the active secretion of extracellular phosphatase in the breakdown of organic P (Aaronson and Patni 1976). In Lake Ontario, "dissolved" APA can be a significant fraction of the total and this has been found in other lakes (e.g. Reichardt et al. 1967).

Table 3 summarizes some of the literature on phophatase measurements when fluorogenic substrates were used. Added substrate levels vary, and those near 0.1 μM MFP were probably limiting so that the corresponding APA values are low compared with the others given. Generally, APA increases with increasing trophic state (defined by chlorophyll concentrations), and with some exceptions, APA normalized for chlorophyll (SAPA) declines. The volcanic New Zealand lakes have very low APA relative to their trophic state (Vincent 1981), while the Erikson lakes have very high values relative to their trophic state (Healey and Hendzel 1980). The former lakes though are often more N than P deficient, so APA should theoretically be low. Even though the Erikson lake 587 is eutrophic, P demand may be high. APA should primarily reflect demand for P rather than trophic state. Based on culture data, Healey and Hendzel (1979) found that SAPA increased with increasing P deficiency with values above 0.005 $\mu M \cdot \mu g$ Chl

TABLE 3. Maximum APA and maximum SAPA from selected aquatic systems as measured with MFP.

Site	MFP (μM)	Temp. (°C)	pH	APA_{max} ($\mu M \cdot h^{-1}$)	$SAPA_{max}$ ($\mu M \cdot \mu g Chl\ a^{-1} \cdot h^{-1}$)	Reference(s)
Erikson 587	10	35	8.5	6.52[a]	0.12	Healy and Hendzel 1980
Erikson 303	10	35	8.5	3.90[a]	0.01	
ELA 303	10	35	8.5	2.31[a]	0.048	
ELA 227	10	35	8.5	0.92[a]	0.031	
ELA 239	10	35	8.5	0.23[a]	0.079	
Erken	0.1	20	8.3	0.15	0.042	Pettersson 1980
Grasmere	0.1	20	8.5	—	0.005	
Hymenjare	0.1	20	8.5	—	0.004	
Stugsjon	0.1	20	8.5	—	0.042	
Magnusjaure	0.1	20	8.5	—	0.042	
Sangre Isle	0.1	20	8.5	0.06	—	Francko 1983
Lawrence	0.1	—[b]	8.5	0.62	—	Wetzel 1981
N. Pacific	0.1	—[b]	8.5	0.007	0.12	Perry 1972
Chesapeake	0.01–0.4	—	8.5	0.01	0.011	Taft et al. 1977
Memphremagog	0.76	23	8.7	0.07[a]	0.013	Sproule and Kalff 1978; Smith and Kalff 1981
Tutaeinanga	0.1	20	8.5	0.001	0.0002	Vincent 1981
Rerewhakaaitu	0.1	20	8.5	0.07	0.003	
Ontario	1.0	35	8.3	0.25	0.06	This study
Jacks	1.0	35	7.3	0.15	0.03	

[a]Particulate APA.
[b]In situ conditions.

$a^{-1} \cdot h^{-1}$ indicative of severe deficiency. All lakes listed in Table 3 would therefore exhibit severe deficiency regardless of trophic state with the exception of eutrophic Grasmere, P-fertilized Hymenjare, and the eutrophic New Zealand lakes. Jacks Lake APA (and SAPA) values were comparable with those measured in Lake Ontario, but turnover times for phosphate are much shorter, and other indicators of P deficiency point to more severe P stress than in Lake Ontario (Lean and Nalewajko 1979; Pick et al. 1984a; Lean et al. 1987).

Many workers express APA per unit chlorophyll (Sproule and Kalff 1978; Healey and Hendzel 1979; Smith and Kalff 1981), but this does not seem justified for Lake Ontario because a significant percentage of the particulate activity is due to the 0.2–1 μm fraction (Table 1) which contains largely bacteria. Most often, little activity is associated with the >12 μm fraction which is almost entirely algal and contains the bulk of the chlorophyll *a* measured in Lake Ontario. The size fractionation data (Table 1) could explain the significant correlation of APA with nanoplankton plus picoplankton data (Fig. 4) and the lack of correlation with total algal biomass. The size fractionation results of Jansson et al. (1981) on an acidified lake also showed the importance of the <5 μm fraction to total APA with the >5 μm fraction contributing only 10% of the total acid phosphatase activity. Francko's (1983) data from north-central Oklahoma lakes suggest that significant APA may be present in particles <1.2 μm in size (as much as 30% between 0.22 and 1.2 μm in eutrophic Sandborn and Sangre Isle lakes). Not examined here was the possible contribution of zooplankton phosphatase to the "dissolved" pool (Rigler 1961; Jansson 1976; Boavida and Heath 1984).

Phosphate additions above 1 μM (well above levels encountered in Lake Ontario) were necessary to achieve 50% repression of APA (Fig. 3) even though 25–30% of the addition was incorporated after 18 h (Lean and Cuhel 1987). This suggests that APA would not track cellular P deficiency very well in the event of sudden P inputs. Possibly, some of the APA measured represents constitutive enzymes rather than P_i suppressible enzymes. The level required for a 50% inhibition in Lake Ontario did not change significantly over the season or at the three stations, suggesting that changing algal or bacterial composition had little influence on the process. Several workers have found that a number of algae produce phosphatases that are not easily inhibited by additions of P_i. This seems particularly true of chrysophytes and cryptomonads (Kuenzler 1965; Aaronson and Patni 1976; Stewart and Wetzel 1982). Cryptomonads are an important component of Lake Ontario throughout the season (Munawar and Nauwerck 1971; Gray 1987). Growing *Ochromonas danica* in excess P_i did not lead to complete repression of intracellular or extracellular phosphatase, and excreted phosphatase increased through the growth phase (Aaronson and Patni 1976). APA was not inducible by P deficiency in *O. vallesiaca* (Healey and Hendzel 1979). There are also reports of algae that do not produce phosphatases at all under conditions of P deficiency (Keenan and Auer 1974). Levels found by other workers to inhibit APA are given in Table 4 along with kinetic data for the enzyme considered. Although the levels vary, they are all higher than maximum SRP measurements in the corresponding aquatic systems.

In agreement with the lack of inhibition of total APA with added P_i, ambient levels of SRP, TP, and TPF did not correlate with APA or SAPA. Other workers though have found reciprocal relationships of SAPA and TP within one lake (Berman 1970; Smith and Kalff 1981), although most found no relationship with ambient SRP (which may also be due to analytical problems with phosphate measurements). Jones (1972b) found a significant correlation between phosphatase

TABLE 4. Half saturation coefficient (K_t), maximum uptake velocity (V_{max}), and added phosphate (P_i) sufficient to induce a specific percent inhibition (I) for phosphatases in natural waters.

Site	K_t (μM)	V_{max} ($\mu M \cdot h^{-1}$)	I (%)	P_i (μM)	Reference(s)
Gardsjon	0.6	—	50	16.13	Jansson et al. 1981
Chesapeake	0.31	0.04	—	—	Taft et al. 1977
Erken	0.28–5.3	—	—	—	Pettersson 1980
East Twin[a]	320	10.4	—	—	Heath and Cooke 1975
Kinneret[a]	0.01–0.7	0.2–1.26	—	—	Berman 1970
N. Pacific	—	—	70	5	Perry 1972
Pluss[a]	1.1	—	80	10	Reichardt et al. 1967
Lake District[a]	—	—	80	32	Jones 1972b
ELA/Erikson	0.2–4	—	—	—	Healey and Hendzel 1979
Ontario	0.48	0.26	50	1	This study

[a]Using *p*-nitrophenylphosphate as substrate.

activity and TP of samples collected from 16 lakes of the English Lake District ranging in trophic state from 1 to- 100 μg Chl $a \cdot L^{-1}$, but not between phosphatase per unit chlorophyll (or per unit bacterial count) and the SRP concentration. Jones (1972b) also found a significant correlation of APA with microbial biomass (estimated from chlorophyll *a* measurements and bacterial plate counts). Kobori and Taga (1979) found a positive relationship between APA and bacterial biomass alone in Japanese coastal waters. Cembella et al. (1984), in a recent review of P metabolism, concluded that "the current practice of using assays of alkaline phosphatase as bioindicators of nutritional status in natural phytoplankton populations is probably reckless and fraught with undesirable complications." The present findings would tend to substantiate this conclusion mainly because of the lack of P_i inhibition at realistic, naturally occurring P_i levels, the persistency of APA after deficiency is overcome, and the variable bacterial contribution to total APA.

Mixing events have an important influence on the measurement of APA in Lake Ontario. The sudden appearance of high APA within the first 5 m only, at 403, on 2 July (Fig. 2) was the result of warm inshore water being blown out into the middle of the lake (Simons and Schertzer 1987), and not the result of midlake conditions. The appearance of APA below the thermocline particularly at the inshore stations is most likely due to downwelling events that occur frequently during the summer. Diurnal changes observed at the end of August at 403 (Fig. 1) were induced by wind events and the propagation of a Kelvin wave (as described in Simons and Schertzer 1987). Diurnal changes in APA were observed in Lake Kinneret (Berman 1970), but the influence of water movements on these observations was not clear. Long-term data from Lawrence Lake clearly showed the influence of lake stability and spring circulation on subsequent APA measurements (Wetzel 1981).

Whether or not APA activity is important in supplying an additional pool of P to phytoplankton depends on the size of the DOP pool that can be hydrolyzed. The maximum APA activity measured in Lake Ontario was 0.25 μM P released $\cdot h^{-1}$ at 35°C. When temperature corrected, using a Q_{10} of 1.4 (which compares with the Q_{10} of 1.6 given by Pettersson and Jansson (1978)), the in situ rate becomes 0.13 $\mu M \cdot h^{-1}$. This rate is achieved with a maximum substrate level of 1 μM MFP; however, the latter levels of hydrolyzable organic P are not likely encountered in situ. Assuming all the DOP is hydrolyzable, given the DOP concentration on 26 August of 0.17 μM and the V_{max} of Fig. 4, a release rate of 0.08 μM is calculated. $K_t + S_n$ on this date was 0.3 μM, but how much of this represents S_n cannot be calculated. The largest V_{max} for phosphate uptake in Lake Ontario was 0.04 μM P $\cdot h^{-1}$ (Lean et al. 1987), which is lower than the maximum possible release rate. Regeneration of P from APA is potentially important. However, because the quantity of hydrolyzable DOP is unknown (but probably small and turning over rapidly), regeneration from this pathway cannot be determined.

There is considerable debate as to the percentage of DOP that is hydrolyzable. This is a critical measurement for the above considerations, but no current method for estimating it is entirely satisfactory. In Chesapeake Bay the bulk of DOP (over 70%) cannot be hydrolyzed according to Taft et al. (1977). Berman (1970) found that 53% of the TP in Lake Kinneret could be hydrolyzed, although these experiments were based on chloroform additions to WLW which must have caused some cell damage. Heath and Cooke (1975) measured high levels of phosphomonoesters in a eutrophic lake using the technique of Strickland and Parsons (1972); however, the percentage that this represented of the total DOP was not given. Herbes et al. (1975) found that no significant amount of P_i could be released from concentrated lake water samples treated with alkaline phosphatase. Similarly, Rigler (1961) was unable to demonstrate hydrolysis of naturally occurring phosphate esters. As pointed out by Cembella et al. (1984), usually only one substrate is tested and added in alkaline phosphatase assays, and the substrate used may not always behave like hydolyzable DOP with respect to the naturally occurring range of phosphatase enzymes, thus underestimating or overestimating APA. In the present study, glycerophosphate and pyrophosphate were not broken down with the same efficiency as MFP. Kinetic experiments under defined laboratory conditions with a wide series of phosphate esters do not give identical V_{max} values for commercial alkaline phosphatase (relative values range from 0.7 to 1.05; Fersht 1977).

In summary, while APA values measured in Lake Ontario are similar to values reported in other mesotrophic systems, APA is not a sensitive indicator of P deficiency. However, APA was significantly correlated with picoplankton and nanoplankton biomass over the season, and particles below 12 μm were responsible for most of the observed activity. High proportions of picoplankton and nanoplankton have been related to nutrient-poor environments. The actual contribution of APA to the

regeneration of P requires further study, but at times of peak APA, P regeneration from this mechanism is potentially important in Lake Ontario.

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Carbohydrate and Protein Content of Lake Seston in Relation to Plankton Nutrient Deficiency

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Pick, F. R. 1987. Carbohydrate and protein content of lake seston in relation to plankton nutrient deficiency. Can. J. Fish. Aquat. Sci. 44: 2095–2101.

Carbohydrate and protein content of seston from Lake Ontario and Jacks Lake, Ontario, were measured during the ice-free season as a means of estimating plankton nutritional status. Despite the similar trophic level of these lakes, protein to carbohydrate ratios were generally above 1 in Lake Ontario, indicating lack of severe phosphorus or nitrogen deficiency, while those of Jacks Lake were always well below 1, indicating severe nutrient stress. However, in Lake Ontario, some discrepancies with other indicators of nutrient status occurred which complicate interpretations of the ratio. The ratio will also not distinguish phosphorus from nitrogen deficiency. On average, 28% (11–80%) of the particulate organic carbon is carbohydrate carbon and 80% (40–100%) of the particulate organic nitrogen is protein-nitrogen in Lake Ontario. Chlorophyll *a* explained 44% of the variation in carbohydrate but only 22% of the variation in protein. Diurnal as well as seasonal and vertical changes in the ratio of protein to carbohydrate were observed.

Les teneurs en hydrates de carbone et en protéines du seston des lacs Ontario et Jacks (Ontario) ont été déterminées au cours de la saison libre de glace comme paramètres d'estimation de l'état nutritionnel du plancton. En dépit de niveaux trophiques semblables dans les deux lacs, le rapport entre les protéines et les hydrates de carbone était généralement supérieur à 1 dans le lac Ontario, indiquant l'absence d'une carence sévère de phosphore ou d'azote, et toujours bien inférieur à 1 dans le lac Jacks, indiquant une carence sévère de matières nutritives. On a cependant noté, pour le lac Ontario, certains écarts avec d'autres indicateurs de l'état nutritionnel, ce qui complique l'interprétation du rapport. Le rapport utilisé ne permet pas non plus de distinguer entre les carences de phosphore et d'azote. En moyenne dans le lac Ontario, 28 % (11–80 %), du carbone organique particulaire est représenté par le carbone des hydrates de carbone et 80 % (40–100 %) de l'azote organique particulaire est représenté par l'azote des protéines. La chlorophyll *a* permet d'expliquer 44 % de la variation notée pour les hydrates de carbone mais seulement 22 % de celle notée pour les protéines. Le rapport entre les protéines et les hydrates de carbone présentait aussi des variations diurnes, saisonnières et verticales.

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While measurements of particulate phosphorus, nitrogen, and carbon are now routine in field studies along with phytoplankton biomass estimates, few measurements of the seston carbohydrate or protein content have been made despite their potential value as indicators of plankton nutritional state (Myklestad and Haug 1972). Healey (1973) suggested that the ratio of protein to carbohydrate could be used as an indicator of nutrient deficiency both for laboratory and field populations of algae. Under batch culture conditions, algae tend to decrease their protein to carbohydrate ratio with the onset of stationary phase (Fogg 1965). Ratios of protein to carbohydrate below 0.7 are likely to indicate extreme nutrient deficiency whereas ratios above 1.2 indicate no deficiency (Healey 1975). Both nitrogen and phosphorus deficiency can bring about such changes in chemical composition (Myklestad and Haug 1972; Healey and Hendzel 1976). On the other hand, under silicon limitation, diatoms do not seem to accumulate carbohydrate. In the field studies of Antia et al. (1963), Healey and Hendzel (1976), Haug et al. (1973), and Rausch (1981a), the seston ratio of protein to carbohydrate decreased during the late stages of algal blooms.

In the present study the seston ratio of protein to carbohydrate was examined in Lake Ontario and Jacks Lake, Ontario, to determine its potential as an indicator of plankton nutritional status. Other measurements of the physiological state of the plankton have been made in both lakes (Pick et al. 1984; Lean et al. 1987; Pick 1987) and were used as independent tests of the method. The two lakes are similar in trophic level (based on chlorophyll *a* and total phosphorus content).

Seasonal, diurnal, and vertical concentrations of particulate protein and carbohydrate were measured from three main stations in Lake Ontario and compared with more routine measurements of the particulate seston (chlorophyll *a*, particulate organic carbon (POC) particulate organic nitrogen (PON) and dry weight). These comparisons were made to determine if the two main cell components give correct estimates of living plankton. For the ratio of protein to carbohydrate to be useful it must be relatively free of detrital interference.

Methods and Materials

Water samples were collected from stations 401 (north shore, 43°53′29″N, 78°15′44″W), 403 (midlake, 43°35′52″N, 78°13′51″W), and 405 (south shore, 43°24′03″N, 78°12′00″W) of Lake Ontario (Lean 1987) during 1982. Water samples from Jacks Lake, a small multibasin lake on the edge of the Canadian Shield (Pick et al. 1984), were collected during 1979, 1980, and 1982. Duplicate aliquots (250–500 mL) were filtered through previously combusted (500°C) Whatman GF/C filters for both carbohydrate and protein analyses. Prescreening for zooplankton was evaluated but considered unnecessary, as their contribution was negligible. A squared filter head was used to decrease the amount of filter area. Filters were frozen immediately for extraction at a later date.

Particulate carbohydrate was measured by the phenol–sulfuric acid method of Dubois et al. (1956). This is more sensitive than the anthrone method and also measures methylated sugars and pentoses. Pentoses give twice the colour yield that hexoses do. However, the structural carbohydrates and storage compounds of cells are largely polysaccarides of hexose units (cellulose, starch, etc.). Nevertheless, the inclusion of pentoses means that the carbohydrate concentrations are maximum values. Excess filter was cut and the sample placed in a screw-cap grinding tube, ground with 1 mL of distilled water, and then made up to 2 mL. Fifty microlitres of 80% phenol was added, the sample vortexed immediately, and 5 mL of concentrated reagent-grade H_2SO_4 dispensed directly and rapidly onto the surface of the liquid. Test tubes, with the caps on, were placed in a 60°C water bath for 20–30 min and then centrifuged at 2600 rpm in an IEC Centra 7 centrifuge for 10 min to eliminate glass fibers. The supernatant absorbance was read at 485 nm using a Pye Unicam spectrophotometer. Control blanks were conducted on squares of ashed GF/C filters. A standard curve was established using reagent-grade glucose so that values of carbohydrate are expressed as micrograms glucose equivalent per litre.

Particulate protein was measured by the Coomassie Brilliant Blue dye-binding method of Bradford (1976) using the dye reagent from Bio-Rad Laboratories. The extraction procedure was in part based on the extensive testing of freshwater algae by Rausch (1981b). As above, the filters were trimmed and placed in screw-cap grinding tubes. Two base sequential extractions were necessary for complete protein recovery. In the first extraction, 1 mL of 0.5 *M* NaOH was added and the filter ground and then incubated for 10 min in an 80°C water bath. This was followed by centrifugation at 2600 rpm for 8 min. The supernatant was removed, made up to 4 mL with distilled H_2O, 1 mL of Bio-Rad reagent was added, and the sample mixed. Within 5 min the absorbance was measured at 595 nm. The above extraction was repeated on the pellet and absorbance of the resulting supernatant read once again. For the standard curve the above procedure was performed on blank ashed (and trimmed) GF/C filters to which concentrations of bovine serum albumin were added. Two extractions were performed as above. Two sets of numbers were therefore obtained for each sample corresponding to the first and second extraction. The latter, on average, yielded 30% more protein. The sum of micrograms protein (bovine albumin equivalent) gave the total micrograms protein in the sample. Values were then corrected for volume of sample filtered. Duplicate measurements varied less than 10% of the mean for both methods. The means of duplicate measurements are presented below.

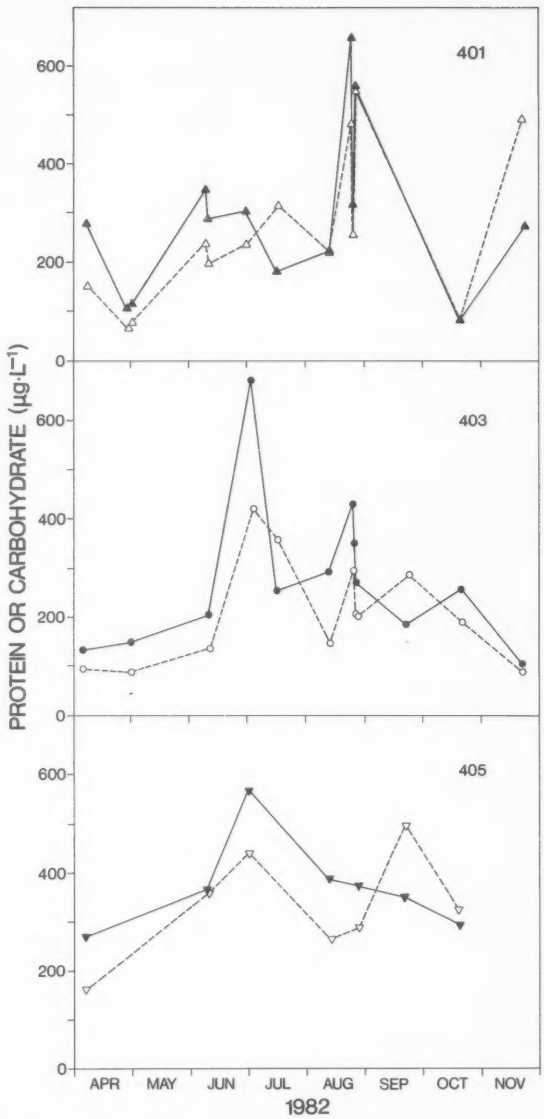

FIG. 1. Epilimnetic seasonal pattern of protein (solid symbols) and carbohydrate (open symbols) concentrations at stations 401, 403, and 405.

POC, PON, and chlorophyll *a* measurements were made by the Water Quality Branch at CCIW (Environment Canada 1979). Dry weight measurements of seston were made on preweighed ashed GF/C filters.

Results

Seasonal Patterns

Particulate carbohydrate values from Lake Ontario ranged from 50 $\mu g \cdot L^{-1}$ near the bottom at the midlake station (403) to a high of 550 $\mu g \cdot L^{-1}$ in the surface waters at the same station in late August. Protein values ranged from as low as 4 $\mu g \cdot L^{-1}$ near

TABLE 1. Protein and carbohydrate content ($\mu g \cdot L^{-1}$) of Jacks Lake summer epilimnetic plankton in relation to POC, PON, and chlorophyll *a*.

Sampling station	Date (d/mo/yr)	Protein	Carbohydrate	Protein: Carbohydrate	POC	PON	POC:PON	Chl *a*
Williams Bay	11/7/79	310	530	0.58	774	67	11.1	3.77
	24/8/79	298	446	0.67	651	58	11.2	1.55
	28/7/80	465	585	0.79	849	102	8.3	6.43
	2/8/80	250	400	0.63	509	57	8.9	1.53
	12/8/80	268	648	0.41	683	63	10.8	2.06
Sharpes Bay	14/7/79	302	524	0.58	590	52	11.3	2.88
	18/8/82	243	794	0.31	716	59	12.1	4.10
Brooks	18/8/82	525	753	0.70	—	—	—	—

the bottom in late fall at 403 to a high of 680 $\mu g \cdot L^{-1}$ in early July at the same station.

At the north shore station (401), epilimnetic concentrations of protein and carbohydrate increased from April through the summer to peak values in late August (Fig. 1). Although both cell components showed a similar trend, the ratio of protein to carbohydrate (Fig. 2) was highest in April (1.75) and declined to below 1 by mid-July before increasing again above 1. The C:N ratio (Fig. 2) was highest when the protein to carbohydrate ratio was lowest. At the midlake station (403), the major peak in protein and carbohydrate occurred in early June, with a smaller peak occuring in late August as at 401 (Fig. 1). The protein to carbohydrate ratio was below 1 on two occasions: the middle of July as at 401 and late in September (Fig. 2). On the former date the C:N ratio had dropped to 5, but by September it was up around 6. The south shore station (405) was sampled less frequently than the other two, but like 403, it showed a peak of both protein and carbohydrate in early July (Fig. 1), and a second peak of carbohydrate occurred in late September.

Midsummer epilimnetic concentrations of carbohydrate from Jacks Lake collected over several years occasionally exceeded 700 $\mu g \cdot L^{-1}$ (Table 1) whereas protein values rarely exceeded 500 $\mu g \cdot L^{-1}$. This resulted in protein to carbohydrate values considerably below 1. C:N ratios are much higher than (9–12) and chlorophyll *a* values are similar to those obtained from Lake Ontario (Gray 1987).

Depth Distribution

During stratification, carbohydrate and protein content of the seston declined with depth through the thermocline at 403 (Fig. 3). Maximum concentrations of both cell components were found within the top 10 m at all times. As summer progressed, the ratio of protein to carbohydrate below the thermocline (50–75 m) declined from a high of 1.8–2.0 at the beginning of July to a low of 0.2 in late November when the water column was still stratified.

Diurnal Changes

Diurnal changes in carbohydrate and protein content of the particulate matter were followed on eight occasions at the three stations. Three examples are shown in Fig. 4. The first two are from 401 on 8–9 June during thermal bar conditions and 28–29 June during breakdown of the thermal bar and complete lake stratification. Protein values on the first occasion ranged from 282 to 428 $\mu g \cdot L^{-1}$ and carbohydrate from 201 to 271 $\mu g \cdot L^{-1}$. Some of these changes could be due to changing water masses.

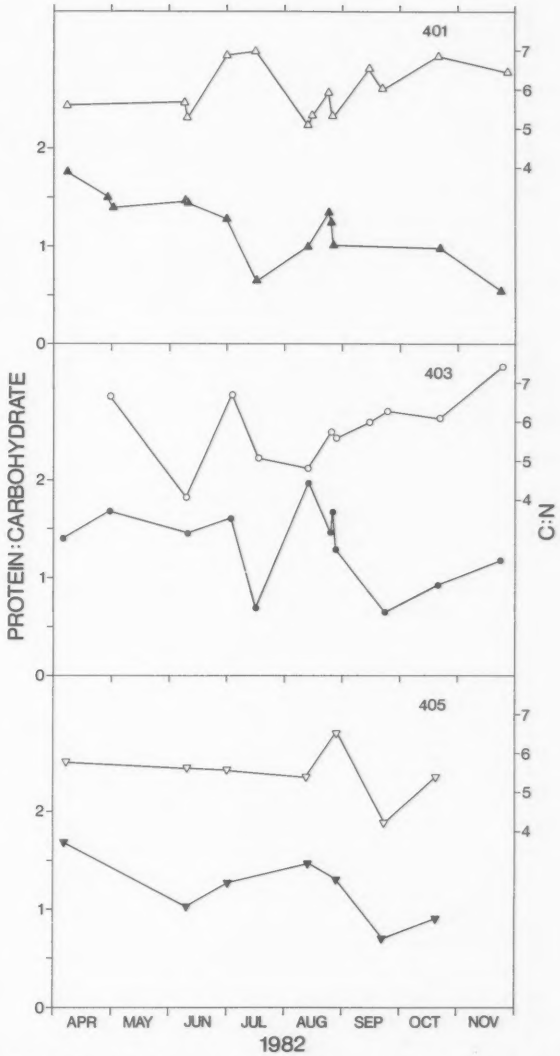

FIG. 2. Seasonal changes in the protein to carbohydrate ratio (solid symbols) and the POC to nitrogen ratio (open symbols) at stations 401, 403, and 405.

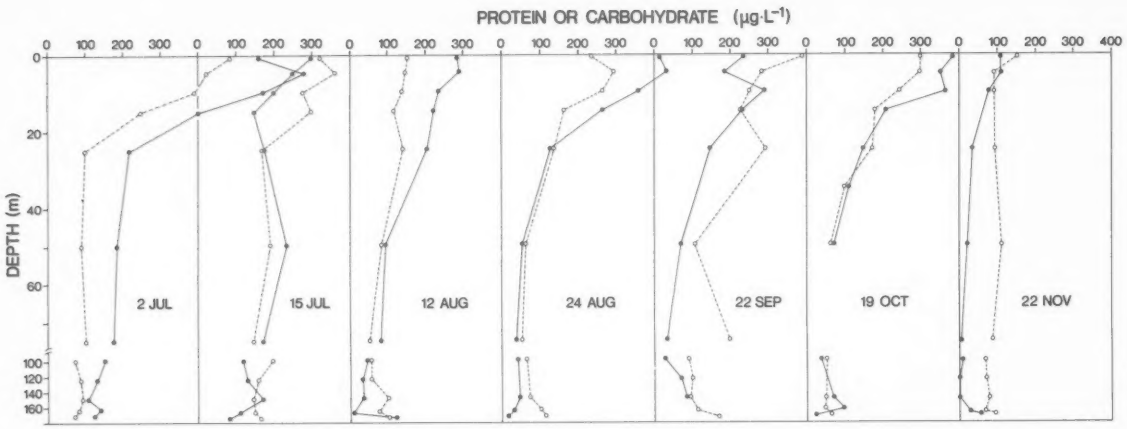

FIG. 3. Depth profiles of protein (solid symbols) and carbohydrate (open symbols) concentrations at the midlake station 403.

Therefore the percent carbohydrate of the POC was calculated to give a better reflection of changing physiological state. This increased from 24% to a high of 44% in late morning. The same pattern was observed on 29–30 June when protein concentrations ranged from 267 to 394 $\mu g \cdot L^{-1}$ and carbohydrate from 240 to 372 $\mu g \cdot L^{-1}$ In the third example, from 19–20 October at 403, the water column was still stratified but the mixing depth was greater. At this time, the peak percentages of carbohydrate occurred in late afternoon and at noon. On the other five occasions during which diurnal changes were measured, all but one showed peak percentages of carbohydrate around noon. The exception was 23–25 August at 403 when little diurnal change in the percent carbohydrate was observed.

Relationship to POC, PON, Chlorophyll *a*, and Dry Weight

Epilimnetic POC correlated significantly with epilimnetic carbohydrate (Fig. 5) for all three stations combined ($r = 0.66$, Table 2). However, 405 alone showed no correlation between the two measurements, while data from 403 showed a significant correlation ($r = 0.84$). When expressed as a percentage of the POC, the carbohydrate carbon content of the seston varied from 11 to 80% over the season and averaged 28%. When expressed as a percentage dry weight of the >1 μm fraction (which would approximate best the retention of Whatman GF/C filters (Sheldon 1972)), carbohydrate content varied from 8 to 32% and protein from 15 to 50% of the dry weight.

Epilimnetic PON correlated significantly with protein, with 46% of the variation in protein accounted for by variations in PON (Fig. 6). The rest of the variation may have been due to the nonliving or detrital component of the particulate matter. If one assumes that all the PON is associated with protein, multiplying PON by 5.71 would yield the protein content of the seston (factor based on the "average" protein of Jukes et al. (1975)). Most of the protein values measured by the Coomassie method fall below this conversion (Fig. 6); therefore, some of the PON is not protein (i.e. nucleic acids, chlorophylls, and other nitrogen-containing compounds). Protein-nitrogen accounted for 40–100% of the PON and averaged 80% over the season.

To obtain some estimate of detrital interference on POC, the chlorophyll *a* content has been regressed against POC by several workers (e.g. Eppley et al. 1977). In Lake Ontario, such regressions result in a *y*-axis intercept of 100 μm $POC \cdot L^{-1}$ for all epilimetic samples collected over the lake (Table 2). However, this high intercept is due to the high intercept values at inshore stations (401 and 405) where sediment resuspension and allochthonous input would be higher. At the midlake station, where 73% of the variation in POC is due to changes in chlorophyll *a*, the y-intercept is only 20 μg $POC \cdot L^{-1}$. Some of this POC would be bacterial biomass and therefore not detrital. A mean bacterial concentration at 403 of $2.52 \times 10^6 \cdot mL^{-1}$ (Pick and Caron 1987) gives an estimate of bacterial carbon of 33 $\mu g \cdot L^{-1}$ (using a carbon content of 0.013 pg $C \cdot cell^{-1}$, quoted by Thompson et al. 1982). Not all bacteria would be caught on a GF/C filter. Therefore, it is unlikely that any of the POC at 403 is detrital. "Detrital" PON for the entire lake was 19.5 $\mu g \cdot L^{-1}$, but again this is primarily due to high values at the inshore stations. Station 403 had a small PON intercept of 7.7 $\mu g \cdot L^{-1}$.

Variations in chlorophyll *a* explained 42% of the changes in carbohydrate but only 22% of the changes in protein. The latter result could be explained by filter fractionation data obtained on the same dates. On average, 56% of the total epilimnetic protein occurred in the fraction passing a 5-μm Nuclepore filter with values ranging from 39 to 70%. The <5 μm fraction contained a smaller but nevertheless significant percentage of the total chlorophyll (30–56%).

Discussion

The ratio of protein to carbohydrate in Lake Ontario during 1982 was usually above 1, and this implies, according to Healey (1975), that the plankton are rarely nitrogen or phosphorus deficient. Exceptions were found in mid-July at 403 when the ratio was around 0.7 and at 401 in November when the ratio was 0.55. On the former date, high phosphatase activity was measured (Pick 1987) and phosphate turnover times were rapid (Lean et al. 1987). However, when phosphatase activity was maximal in late August at 403 the protein to carbohydrate ratio was high (1.3–1.7) and the C:N ratios were low (5–6). Therefore, on this date, while other measurements indicated phosphorus deficiency and nitrogen sufficiency, the protein to carbohydrate ratio indicated no nutrient deficiency. The ratio at 401 was low in November when other indicators of deficiency showed no phorphorus or nitrogen stress. This was likely the result of deep mixing conditions bringing up water from below

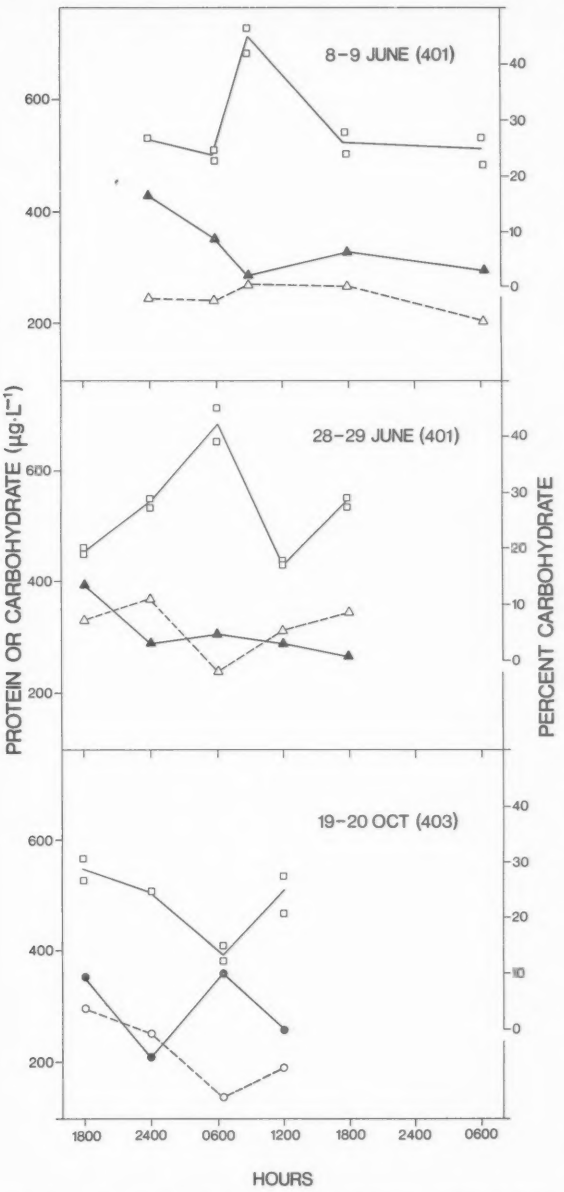

FIG. 4. Diurnal changes in carbohydrate and protein content on three dates. Symbols as in Fig. 1. Carbohydrate carbon expressed as a percentage of POC (□).

the thermocline where ratios by the end of the summer were low.

The ratio of protein to carbohydrate below the thermocline at the midlake station declined through the summer (Fig. 3), but this could not be the result of nutrient deficiency of either nitrogen or phosphorus. Protein appeared to be broken down more rapidly than carbohydrate. The phenol–sulfuric method used here would include the carbohydrates of the fibrillar material described by Leppard et al. (1977), which is not readily

TABLE 2. Determination of dependence of cell components (protein, carbohydrate) on biomass indicators (chlorophyll *a*, POC, PON). Probability based on correlation coefficients.

	n	*r*	*y*-intercept	Slope	$p <$
		Chlorophyll a *vs. protein*			
Whole lake	73	0.47	169.3	30.0	0.001
403	32	0.34	164.7	26.9	0.05
401	25	0.57	109.3	49.9	0.005
405	16	0.39	243.5	30.1	ns
		Chlorophyll a *vs. carbohydrate*			
Whole lake	73	0.65	112.5	36.4	0.001
403	32	0.81	36.4	50.0	0.001
401	25	0.56	98.8	45.6	0.005
405	16	0.36	245.1	15.9	ns
		PON vs. protein			
Whole lake	73	0.68	78.9	3.3	0.001
403	32	0.62	78.4	3.1	0.001
401	24	0.69	48.8	4.0	0.001
405	17	0.69	115.6	2.9	0.005
		POC vs. carbohydrate			
Whole lake	73	0.66	98.2	0.45	0.001
403	32	0.84	39.6	0.56	0.001
401	24	0.52	116.1	0.40	0.01
405	17	0.31	270.3	0.16	ns
		Chlorophyll a *vs. PON*			
Whole lake	74	0.78	19.5	10.7	0.001
403	34	0.81	7.7	12.7	0.001
401	24	0.67	22.9	10.9	0.001
405	16	0.66	38.3	7.9	0.01
		Chlorophyll a *vs. POC*			
Whole lake	74	0.79	100.5	67.9	0.001
403	34	0.85	19.8	82.3	0.001
401	24	0.69	112.6	77.2	0.001
405	16	0.80	78.1	65.5	0.001

broken down through microbial activity (K. Burnison, National Water Research Institute, Burlington, Ont., pers. comm.).

There are therefore some discrepancies with metabolic indicators of nutrient status which need to be carefully examined in each aquatic system before the ratio can be used as an indicator of nutrient deficiency. In particular, upwelling events which bring to the surface layers deep water with a low protein to carbohydrate ratio need to be considered.

Measurements from Jacks Lake resulted in ratios of protein to carbohydrate consistently below 1 and as low as 0.3 in late summer, indicating severe nutrient stress. This is corroborated by other physiological measurements pointing to severe phosphorus deficiency and possibly nitrogen deficiency in late summer as well (Pick et al. 1984). Despite similarities in total chlorophyll and phosphorus concentrations, the plankton of Jacks Lake was considerably more stressed for nutrients than Lake Ontario plankton.

Myklestad (1977) implied that protein to carbohydrate ratios above 1 indicate rapidly growing populations. However, other measures of growth (rates of sulfur incorporation into protein) suggest that Jacks Lake growth rates are in fact higher than in Lake Ontario. Making inferences about growth rates from the protein to carbohydrate ratio of the seston seems unwarranted. However, the ratio can be used as an indicator of nutrient status in Jacks Lake and probably other small lakes where upwelling of deep water during the summer is rare. The ratio is especially

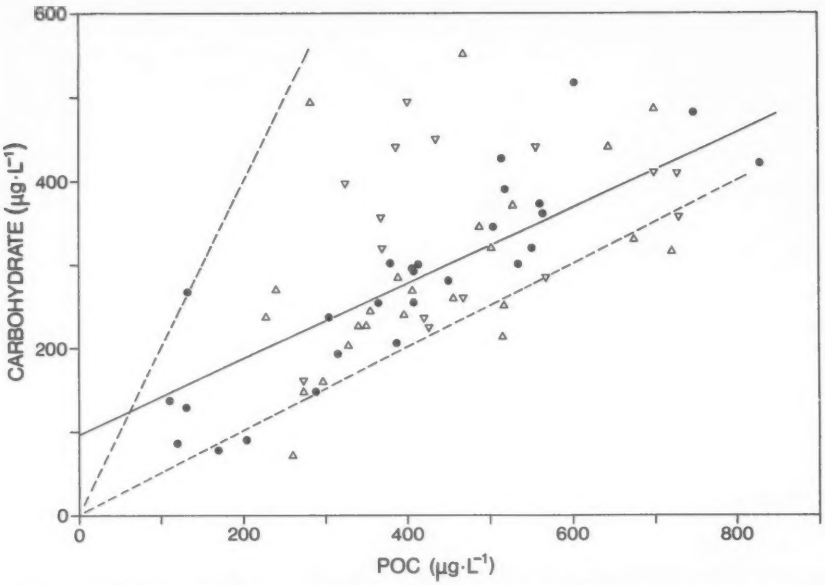

FIG. 5. Carbohydrate concentration as a function of POC at stations 403 (●), 401 (△), and 405 (▽). The solid line is the regression. The upper broken line represents an 80% carbohydrate carbon content of POC and the lower broken line a 20% content.

useful because it is easier to measure than metabolic indicators of nutrient status that may require the use of isotopes.

In Norwegian fjords, net plankton (>25 μm) protein to carbohydrate ratios were in a similar range over the season (0.48–1.83), with the spring bloom characterized by a rapid decrease in the ratio (Haug et al. 1973). However, some of this was attributed to changes in species composition. Samples rich in dinoflagellates had typically low protein to carbohydrate ratios, due to the high content of insoluble wall polysaccharides. Dinoflagellates are rarely an important component of Lake Ontario phytoplantkon (Munawar and Nauwerk 1971; Gray 1987) or Jacks Lake, so although this problem was not important in the present study, it should be considered in other systems.

In cultures, the range of protein to carbohydrate ratios is considerably greater (0.16–8.8 for *Chlorella pyrenoidosa* cited in Healey (1973)). In addition to total nutrient supply, the N:P ratio leads to changes in the ratio as shown by Myklestad (1977): for two marine diatoms an increase in N:P in the medium resulted in a decrease in the protein to carbohydrate ratio when cells were in exponential growth. This might suggest that the ratio is more sensitive to phosphorus limitation than nitrogen limitation. On the other hand, from an extensive comparison of indicators of nutrient deficiency in natural populations, Healey and Hendzel (1980) suggested that the protein to carbohydrate ratio was more sensitive to nitrogen limitation. However, none of their ratios were below 1 such as found in Jacks Lake where phytoplankton are more phosphorus than nitrogen deficient (Pick et al. 1984). The ratio is therefore not very useful in separating nitrogen from phorphorus deficiency.

As one might expect, the carbohydrate content of the POC was quite variable even though there was a strong correlation over the season between the two measurements. Carbohydrate accounted for 11–80% of the POC in Lake Ontario; the remaining percentage would be due to varying amounts of carbon in mainly protein and lipids. The latter were not measured in this study because they contribute at the most 10% of the dry weight of algal cells. Summer data from Jacks Lake gave a smaller range of 27–44% but Jacks Lake has a much higher "detrital" component (F. R. Pick, unpubl. data) to the POC than Lake Ontario so that the percentages are actually higher.

Chlorophyll *a* explained 42% of the variation in carbohydrate but only 22% of the variation in protein. The latter result could be explained by protein size-fractionation data which showed that over half the particulate protein was found in the <5 μm fraction. This fraction contains a smaller percentage of the total chlorophyll (30–56%). Most of the protein is in small organisms, either heterotrophic or autotrophic, but the autotrophic biomass is the most important (at least in Lake Ontario). In addition, organisms other than phytoplankton would contribute to the carbohydrate and protein content of the seston (bacteria, microzooplankton). However, their total biomass is considerably less that the total biomass of phytoplankton.

Diurnal changes in the protein and carbohydrate content of natural populations have been reported by Gibson (1978) for a blue-green population and Frempong (1983) for *Ceratium*-dominated populations. Based on one day's sampling of Lake Constance, T. Rausch (Universitat Gesamthoschule Essen, Germany, unpubl. data) found that carbohydrate content (percentage of ash-free dry weight) peaked at noon (34.8%) and declined through the afternoon (1700, 29.7%) prior to nightfall. The same pattern was also observed in Lake Ontario on several dates over the season (Fig. 4), although the data are complicated by the possibility of changing water masses. Experiments conducted by Cuhel and Lean (1987) on the subcellular partioning of recently incorporated [^{14}C]bicarbonate in Lake Ontario clearly show that protein synthesis continues through

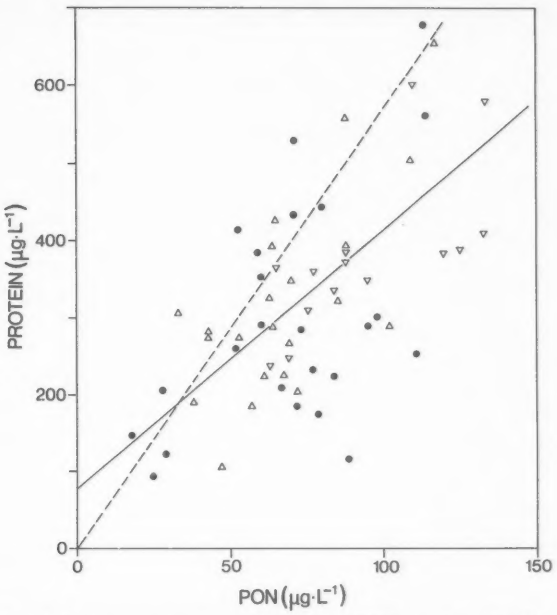

FIG. 6. Protein concentration as a function of PON at stations 403 (●), 401 (△), and 405 (▽). The solid line represents the regression and the broken line represents the conversion factor of 5.71 used to convert nitrogen to protein.

the night at the expense of carbohydrate produced during the light period. Indeed their data (Cuhel and Lean 1987, fig. 6) suggest that the cells anticipate the onset of darkness in preparation for this interconversion, even when subjected to a constant light intensity.

Although further diurnal experiments are required, it is likely that the chemical composition of plankton changes on a diurnal as well as on a seasonal basis in many aquatic systems. This means that when measuring the ratio of protein to carbohydrate the time of sampling is critical, and this has not been always considered in previous investigations. Finally, in the light of laboratory experiments on the effect of algal composition on the growth of herbivores (Scott 1980), the implications for zooplankton grazing of diurnal changes in the protein to carbohydrate ratio of seston need to be evaluated.

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Protein Synthesis by Lake Plankton Measured Using in situ Carbon Dioxide and Sulfate Assimilation

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Cuhel, R. L., and D. R. S. Lean. 1987. Protein synthesis by lake plankton measured using in situ carbon dioxide and sulfate assimilation. Can. J. Fish. Aquat. Sci. 44: 2102–2117.

Sequential 4- to 6-h in situ measurements of carbon dioxide and sulfate uptake showed midday deepening of the depth of P_{max} and photoinhibition of upper water column samples. Analysis of subcellular fractions accentuated total uptake measurements, with net protein synthesis providing a direct measure of growth. The percentage of carbon assimilated into protein was smallest at the depth of maximum photosynthesis and increased with light limitation. Summed incubations agreed well with all-day deployments for total carbon fixation and protein synthesis. Assimilation numbers were consistently low (<2.5 g C·g Chl $a^{-1}\cdot h^{-1}$ with integrated (0–20 m) areal production of 616–1467 mg C·m^{-2} and 7.5–32.4 mg S·m^{-2} during the light day. Nonreductive sulfate assimilation (predominantly ester-SO_4^-) accounted for up to 40% of the total sulfate uptake when diatoms predominated. Protein synthesis measured with ^{35}S (200–1000 mg protein·m^{-2} during the light day) increased 57–89% overnight. Hourly rates were similar during light and scotophase incubations. Night metabolism substantially altered the biochemical composition (e.g. protein, lipid, and carbohydrate) of the plankton with respect to newly incorporated carbon. Combined plant-specific $H^{14}CO_3^-$ and general microbial $^{35}SO_4^{2-}$ techniques suggested algal dominance in the mixed layer.

Des mesures séquentielles sur place de 4 à 6 h de l'absorption de gaz carbonique et de sulfate ont montré qu'il y a en milieu de journée augmentation de la profondeur de P_{max} et photoinhibition d'échantillons venant de la couche supérieure de la colonne d'eau. L'analyse des fractions subcellulaires a fait ressortir les mesures d'absorption totale, la synthèse nette de protéines fournissant une mesure directe de la croissance. Le pourcentage de carbone assimilé dans la protéine a été le plus faible à la profondeur où la photosynthèse est maximale et a augmenté en fonction de la limitation de la lumière. La somme des incubations concordait bien avec les incubations pour toute la journée quant à la fixation du carbone total et la synthèse de protéines. Les taux d'assimilation ont été uniformément faibles ($<2{,}5$ g C·g Chl $a^{-1}\cdot h^{-1}$), la production surfacique intégrée (de 0 à 20 m) allant de 616 à 1467 mg·m^{-2} de C et de 7,5 à 32,4 mg·m^{-2} de S pendant les heures de luminosité. L'assimilation du sulfate qui ne se fait pas par réduction (surtout de l'ester-SO_4^-) représentait jusqu'à 40% de l'absorption totale du sulfate lorsque les diatomées étaient en grand nombre. La synthèse de protéines mesurée avec le ^{35}S (200 à 1000 mg·m^{-2}w de protéine pendant les heures de luminosité) a augmenté de 57 à 89% pendant la nuit. Les taux horaires étaient semblables lors des incubations à la lumière et à l'obscurité. Le métabolisme pendant la nuit a modifié de façon importante la composition biochimique (p. ex. protéines, lipides et hydrates de carbone) du plancton pour ce qui est du carbone récemment incorporé. Les techniques particulières aux plantes utilisant du $H^{14}CO_3^-$ combinées aux techniques microbiennes générales faisant appel au $^{35}SO_4^{-2}$ ont semblé indiquer qu'il y avait dominance des algues dans la couche de mélange.

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The biochemical composition of newly formed particulate material resulting from phytoplankton growth is modulated by light, temperature, species composition, and the nutritional state of the plankton. Recently developed methods for measurement of macromolecular synthesis by phytoplankton permit analysis of specific end products of carbon fixation (e.g. protein, carbohydrate, and lipid) and may provide a means of identifying nutrient deficiency in phytoplankton by accumulation of carbon in carbohydrate and lipid storage products beyond daily growth requirements (Antia et al. 1963; Antoine and Tepper 1969; Strickland et al. 1969; Hobson and Pariser 1971; Konopka and Schnur 1981). The relative content of protein, lipid, and carbohydrate in phytoplankton may also affect the value of microplankton as a food source for herbivores (Scott 1980).

Sulfate incorporation into protein provides a quantitative measurement of net protein synthesis by microplankton (Bates 1981; Cuhel et al. 1982). In combination with carbon assimilation studies it enables detection of biomass turnover in circumstances when algal growth is slow or absent (Cuhel et al. 1984). Since sulfate is taken up as needed, the method can be used to demonstrate net protein synthesis by microplankton at night, a

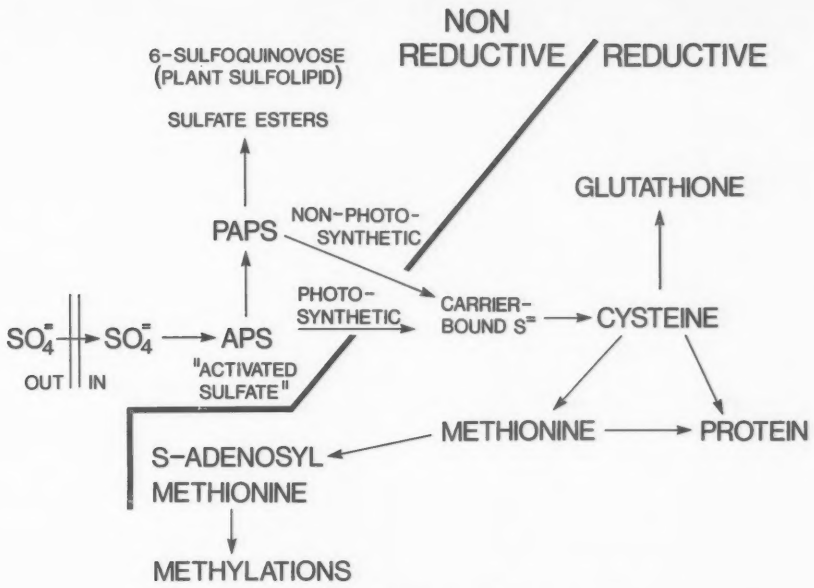

FIG. 1. Schematic pathways of sulfate assimilation in microorganisms.

phenomenon which is closely linked to diel patterns of carbon metabolism. In addition, total sulfate uptake and the ratio of reductive to nonreductive sulfate assimilation (see below) give useful information for construction of geochemical cycling models in aquatic systems.

The combined measurements of sulfate uptake and subcellular incorporation patterns for both carbon and sulfur were applied to several specific problems or questions in lake productivity analysis: (1) investigation of effects of sampling time-of-day and in situ incubation time on productivity estimation; (2) determination of areal rates of reductive sulfate assimilation and protein synthesis, with comparison with ^{14}C-labeled bicarbonate uptake and incorporation patterns; and (3) measurement of night protein synthesis by ^{35}S-labeled sulfate incorporation into protein and related night changes in carbon metabolism following in situ incubation. Because in situ methods take into account small-scale temperature gradients, light quality, and differences in phytoplankton species composition, abundance, and light adaptation with depth, they may provide more accurate estimates of production than obtained with artificial light incubators. In most cases, in situ studies were accompanied by time-course light intensity experiments (Cuhel and Lean 1987).

Pathways of Sulfate Assimilation

Sulfate transport is an energy-requiring process which concentrates sulfate against an external–internal concentration gradient (Deane and O'Brien 1975; Jeanjean and Broda 1977; Cuhel et al. 1981). Once inside the cell, the relatively inert sulfate ion must be activated by ATP (Fig. 1); the activated sulfate (APS or PAPS) is subsequently available for reductive assimilation into cysteine, methionine, and sulfur-containing peptides (e.g. glutathione) and protein (see Tsang and Schiff 1975). Alternatively, several important nonreductive pathways of sulfur assimilation have been described, including synthesis of the plant sulfolipid (Benson 1963) which is an obligate requirement for photosynthetic electron transport and hence a component of all photosynthetic membrane structures (Menke et al. 1976; Sinensky 1977). A second major sulfur-containing product is acidic sulfate esters of polysaccharides, common among diatoms and red and brown algae (Ramus 1974; Percival et al. 1980). Both sulfolipid synthesis and ester sulfate synthesis are carried out by algae to the greatest extent, although some bacterially derived sulfate esters have been reported (Fitzgerald 1976). Finally, the involvement of *S*-adenosylmethionine (SAM) in methylation reactions is shown in Fig. 1: although the sulfur atom of methionine is not transformed in the methylations, there is a broad range of environmentally important products arising from SAM-catalyzed methylations which may be investigated through studies with radiolabeled methionines.

The geochemical fate of biogenic sulfur in the water column and in sediments depends on the degree to which the sulfur is reduced. Most biomass sulfur is fully reduced to the level of sulfide (S^{2-}) and can be either incorporated directly by decomposers after protein hydrolysis or released to the environment as H_2S (from amino acid fermentation) or as volatile sulfur compounds (e.g. dimethyl sulfide) to the atmosphere. The latter process accounts for about 30 Tg $S \cdot yr^{-1}$ in the global atmospheric sulfur cycle (Andreae and Raemdonck 1983). The oxidized forms mentioned above are more refractory to degradation and probably become involved in sedimentary processes. By virtue of its hydrolysis-resistant C—S bond, the plant sulfolipid may persist in sediments and provide a marker for phytoplankton sedimentation. More quantitatively significant is the ester sulfate of acidic polysaccharides (Nriagu and Soon 1985): its labile —C—O—SO_3^- linkage is susceptible to arylsulfatase-catalyzed hydrolysis in sediments (Nriagu and Soon 1984); combined with its high proportion of total sulfur fixation in some circumstances can result in substantial inputs of inorganic sulfate required for sedimentary sulfate reduction. We have therefore considered sulfate assimilation in the context of

both total and reductive (i.e. excluding sulfate esters and sulfolipids) forms. Whole-cell sulfate uptake measurements (cf. Jassby 1975; Campbell and Baker 1978; Monheimer 1978b) do not differentiate between reductive and nonreductive assimilation, but the distinction may be of value in models of biogenic reduced sulfur inputs for acid rain and related considerations.

Materials and Methods

Water samples were collected from the CSS *Limnos* in 5-L Niskin bottles deployed on a rosette sampler with temperature sensor. The samples, collected from fixed depths, were drawn into steam-cleaned 300-mL BOD bottles and spiked with either ^{14}C-labeled bicarbonate (2 GBq·mnol^{-1}, 20 dpm·ng C^{-1} final specific activity) or ^{35}S-labeled sulfate (carrier-free, 125 dpm·ng S^{-1} final specific activity). The bottles were returned to the original depths on a mooring several hundred metres from the ship. For back-to-back incubations, three moorings were deployed, with one reserved for an all-day incubation. Short-term experiments were sequentially deployed and removed from the remaining two moorings. Subsurface light intensity was determined with a submersible LiCor quantum sensor near local noon, and total daily light flux was calculated from pyroheliometer data.

In general, preincubation manipulations were carried out in subdued light before dawn. Unless specified otherwise, "^{14}C" and "^{35}S" refer to filter-retainable radioactivity derived from labeled sodium bicarbonate and sodium sulfate, respectively.

At the end of each incubation, ^{14}C- and ^{35}S-labeled samples were filtered through Whatman GF/F filters using the punch funnel described in Cuhel et al. (1981) to reduce isotope adsorption. The filters were then frozen (−20°C) for subsequent laboratory processing. The subcellular fractionation procedure used to separate low molecular weight (LMW), alcohol-soluble protein, lipids, hot trichloroacetic acid (HTCA) soluble material, and residue protein is described in Cuhel et al. (1984).

The long turnover time for sulfate (>10 yr) requires the use of high radioisotope activities. However, the subcellular fractionation procedure isolates contaminating, unfixed sulfate in the LMW fraction and it is easily removed by barium precipitation. For this reason, low blanks in the other fractions can be routinely obtained without the rigorous isotope preparation employed by Bates (1981).

Radioisotopes were obtained from New England Nuclear Corp. and Amersham Searle. Filters for whole-cell uptake and aliquots of derived fractions were counted in PCS (Amersham Searle) by liquid scintillation on a Searle Mark III using the external standards method of quench correction. All data for ^{14}C-labeled bicarbonate uptake were corrected for isotope discrimination using the factor of 1.06 recommended by Steemann-Nielsen (1952). Incorporation of ^{35}S-labeled sulfate into biomass occurs without isotope discrimination (McCready et al. 1975).

Synoptic analyses of dissolved nutrients and particulate carbon, nitrogen, phosphorus, and chlorophyll *a* were provided by the Water Quality Laboratory, Canada Centre for Inland Waters, Burlington, Ont.

Composition of the Subcellular Fractions

This study relies on a subcellular fractionation procedure which separates classes of molecules based on their sequential solubilization by a variety of relatively specific solvents under appropriate extraction conditions (Roberts et al. 1963). Because it is critical to understand possible ambiguities arising from the actual composition of particular intracellular fractions, an overview of the types of labeled molecules expected in each fraction is given below.

Low molecular weight (LMW)

The cold trichloroacetic acid (TCA) soluble fraction contains a wide variety of metabolic intermediates and all the inorganic ions. Sugars and sugar phosphates, amino acids and peptides, nucleotides, and vitamins and coenzymes are found in this fraction. Precipitation of inorganic sulfate with barium leaves in solution the "LMW organic-S" component of ^{35}S-labeled samples. The loss of cysteine or methionine is negligible.

Alcohol-soluble protein (EtOH)

Samples labeled with ^{35}S can contain a significant amount of label in the alcohol-soluble, ether-insoluble portion of the lipid extract. The aqueous phase of the partitioned extract contains proteins with amino acid compositions similar to that of the residue protein (Roberts et al. 1963) and probably consists of more hydrophobic membrane proteins such as permeases and electron transport system proteins. The proportion of ^{14}C incorporated into this fraction is trivial (<1%), so for ^{14}C it is not separated and is therefore included in the lipid fraction.

Lipid

This contains ether-soluble membrane lipids, neutral fats, and sterols. Sulfolipid, an integral part of photosystem II, found only in photosynthetic organisms, is contained in this fraction.

Hot TCA-soluble (HTCA)

Mono- and oligosaccharides from the hot acid hydrolysis of polymeric carbohydrates and mono- and oligonucleotides from hydrolysis of ribonucleic acids (RNA) and deoxyribonucleic acids (DNA) are the primary constituents of the HTCA material. Hydrolyzed bacterial cell walls (hexosamines) and a small amount of protein can also appear in this fraction. In ^{35}S-labeled samples the hydrolysis of sulfated polysaccharides releases inorganic sulfate which can be precipitated with barium, subdividing HTCA into "ester-SO_4^-" and "HTCA organic-S" components.

Protein

The final residue contains the bulk of cellular protein, but cellulose is also resistant to the above treatments and is included in this fraction. Although cellulosic cell walls are not common in algae, they can occur in some species of the Chlorophyceae, Chrysophyceae, Dinophyceae, Prasinophyceae, Rhodophyceae, and Xanthophyceae (Sournia 1981).

While replicate samples generally agree very well (cf. Cuhel et al. 1984), instances of mismeasurement, filter inefficiency, etc., do occur. We emphasize the fact that within an experimental treatment, subcellular distribution, as a percentage of total fixed label in specific fractions, is independent of the total amount of isotope retained on the filter. The precision of subcellular distribution is in fact better than that of total uptake, which allows resolution of smaller differences among samples and can help identify aberrant whole-cell uptake data. All data reported herein for total uptake are the sum of the derived fractions. Unprocessed filters labeled with ^{14}C were regularly counted to verify recovery. We can assume a similar recovery for ^{35}S in the replicate samples, since the fractionation procedure was essentially identical.

TABLE 1. Vertical profiles of temperature, chlorophyll *a*, particulate carbon and nitrogen, carbohydrate, protein, dissolved nitrate plus nitrite, and soluble reactive phosphorus ($\mu g \cdot L^{-1}$). Data are for near-dawn samples.

Depth (m)	Temp. (°C)	CHL *a*	POC	PON	Carbohydrate	Protein	NO_3 $+NO_2$	SRP
				8 June 1982, station 401				
1	10.46	2.9	352	64	227	394	280	1.0
5	9.84	3.3	358	65	244	428	282	0.8
10	7.56	4.0	394	69	286	362	292	0.9
15	6.15	4.0	325	59	233	362	310	0.9
30	5.43	3.0	276	50	179	286	332	1.5
				1 July 1982, station 405				
1	15.50	7.9	76	134			199	1.4
5	15.50	9.3	762	139	353	583	204	1.6
10	14.40	9.2	629	115			270	1.4
15	9.70	9.2	629	115			270	1.3
29	6.20	5.8	345	55			332	1.0
				26 August 1982, station 403				
1	12.53	5.1	349	68			213	0.2
5	12.53	3.4	387	69	205	268	210	0.2
10	12.43	4.0	384	74			206	0.5
15	12.04	3.2	465	95			211	0.2
25	4.82	1.3	230	37			302	0.6

Results

Diurnal cycles of photosynthetic capacity (Jorgensen 1966; Prézelin et al. 1977) and incorporation of carbon into macromolecules (Morris and Skea 1978; Cuhel et al. 1984) are well documented. The rhythms may result from mixing in the water column and exposure to variable light fields (Marra 1978a, 1978b); hence, all-day in situ incubations which retain the sample at a fixed depth for prolonged periods may introduce artifacts in total production measurement. Since it is not always practical to make repeated in situ deployments during the day, on several occasions we compared total uptake and subcellular incorporation patterns of ^{14}C-labeled bicarbonate from three sequential in situ incubations with results from samples incubated all day. Physical and standing crop measurements of the stations are summarized in Table 1.

The first example is from inshore station 401 on 8 June 1982 when the water column was weakly stratified under thermal bar conditions (Simons and Schertzer 1987). Subsurface maxima for total carbon fixation and incorporation into protein and lipid were evident during each incubation period (Fig. 2). Photoinhibition of ^{14}C-labeled bicarbonate uptake was most pronounced in midday samples at 1 and 2.5 m. The $\%C_{prot}$, an indicator of photoinhibition in light intensity experiments (Cuhel and Lean 1987), displayed the most marked increase at the surface in the late afternoon incubation. At this time, although the magnitude of the subsurface maximum was less pronounced, the hourly rate of photosynthesis was reduced at all depths to values similar to early morning incubations. Incorporation of CO_2-C into protein was much more uniform with depth and time of day than was total carbon fixation or incorporation into lipids.

The all-day incubation yielded lower values for carbon dioxide uptake and incorporation than the sum of the sequential incubations, although the differences were generally <25%. Discrepancies were greatest below 5 m, but there was very little difference in the %C among fractions, shown for $\%C_{prot}$ in Fig. 2.

Net protein synthesis was measured using ^{35}S-labeled sulfate for the all-day incubation. Vertical profiles for total uptake and subcellular distribution of CO_2-C and SO_4-S (Fig. 3) were similar in the depth of the principal subsurface maximum for total uptake and the shape of the protein production profile. Total light:dark uptake ratios for sulfate increased from the surface to a maximum at the productivity maximum. At 10 m and below the ratio was about half that at P_{max}. Below 45 m, microbial growth was essentially undetectable by these techniques.

Ester sulfate dominated the subcellular distribution of sulfur, comprising up to 40% of the total fixed sulfur. Ester-S was far more significant in the upper water column: both $\%S_{ester}$ and total ester decreased rapidly with depth (Table 2). The light:dark ratio of ester sulfate synthesis was also depth dependent. Sulfur incorporation into protein was a relatively constant proportion of total sulfur metabolism in the upper 12.5 m, below which it increased. Samples from deeper in the water column had increasing proportional incorporation of sulfate into protein in the dark (Table 2).

Whole-cell and protein C:S ratios were similar, increasing from 50 at 1 m to almost 90 at 10 m (Fig. 3). Below this depth, both decreased rapidly. The difference between total-C:total-S (whole cell) and total-C:reduced-S emphasized the large contribution of ester sulfate to total sulfur uptake, especially in the upper 10 m. The total-C:reduced-S ratio is more appropriate to physiological interpretation because ester-SO_4^- is generally associated with extracellular polysaccharides; hence, total-C:reduced-S will be used for the remainder of this paper.

The in situ experiment described above took place during stratification at the inshore station. The physical instability may have resulted in sampling of different plankton populations at

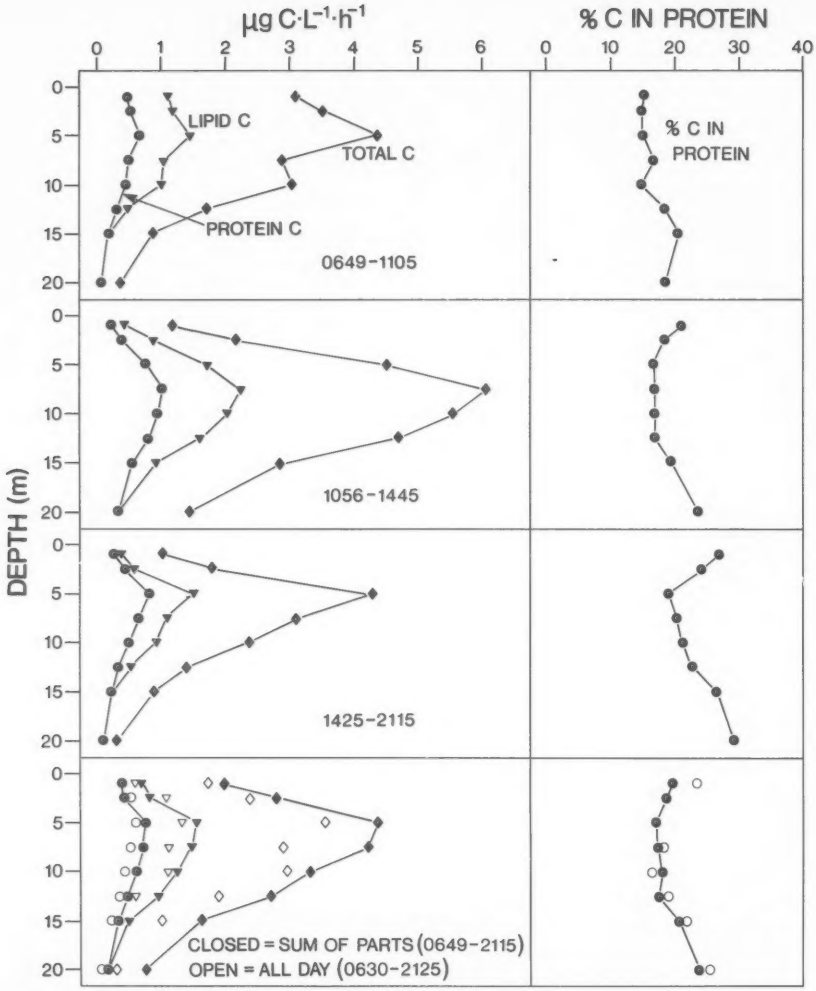

FIG. 2. Total carbon uptake and its incorporation into lipid and protein during back-to-back in situ incubations at station 401 on 8 June. The proportion of carbon incorporated into protein is shown in the right-hand panels. The bottom panels show the sum of the three incubations (solid symbols) compared with all-day (0630–2125) in situ incubation (open symbols).

each depth throughout the day. For accurate comparison of sequential and all-day incubations, it is necessary that similar populations are repetitively sampled at each depth. The following examples were obtained at stations with well-defined thermoclines which restricted mixing to the epilimnion.

A three-part back-to-back in situ deployment at the south-shore station (405) on 1 July 1982 represented conditions of strong stratification and high chlorophyll *a* concentration (Table 1). Subsurface maxima for total carbon fixation and its assimilation into lipid and protein occurred only during the midday incubation (Fig. 4), and there was only slight evidence of photoinhibition based on $\%C_{prot}$, despite nearly 1800 µEinst.·m^{-2}·s^{-1} of incident solar radiation at noon. Photosynthesis fell off rapidly below the level of P_{max} (depth of 1% light penetration, 10.9 m) accompanied by increased proportional incorporation of carbon into protein indicative of light limitation. In contrast with the previous example, the agreement of summed sequential incubations with the all-day deployment was excellent for total photosynthesis and subcellular carbon incorporation patterns.

Depth profiles of total sulfate uptake and incorporation into protein and ester components differed from those for carbon only in the morning incubation (Fig. 5) when the rate of decrease with depth was not as steep and the depth of maximum protein synthesis was slightly deeper for sulfur. In all other respects the two measurements provided very similar results. Protein-S from the all-day deployment agreed well with the sum of the sequential experiments, and the lower all-day total sulfur was attributable to lower ester sulfate labeling. As for the previous example, ester sulfate was much less significant deeper in the water column, and the proportion of sulfur incorporated into protein increased with depth in all cases (Fig.

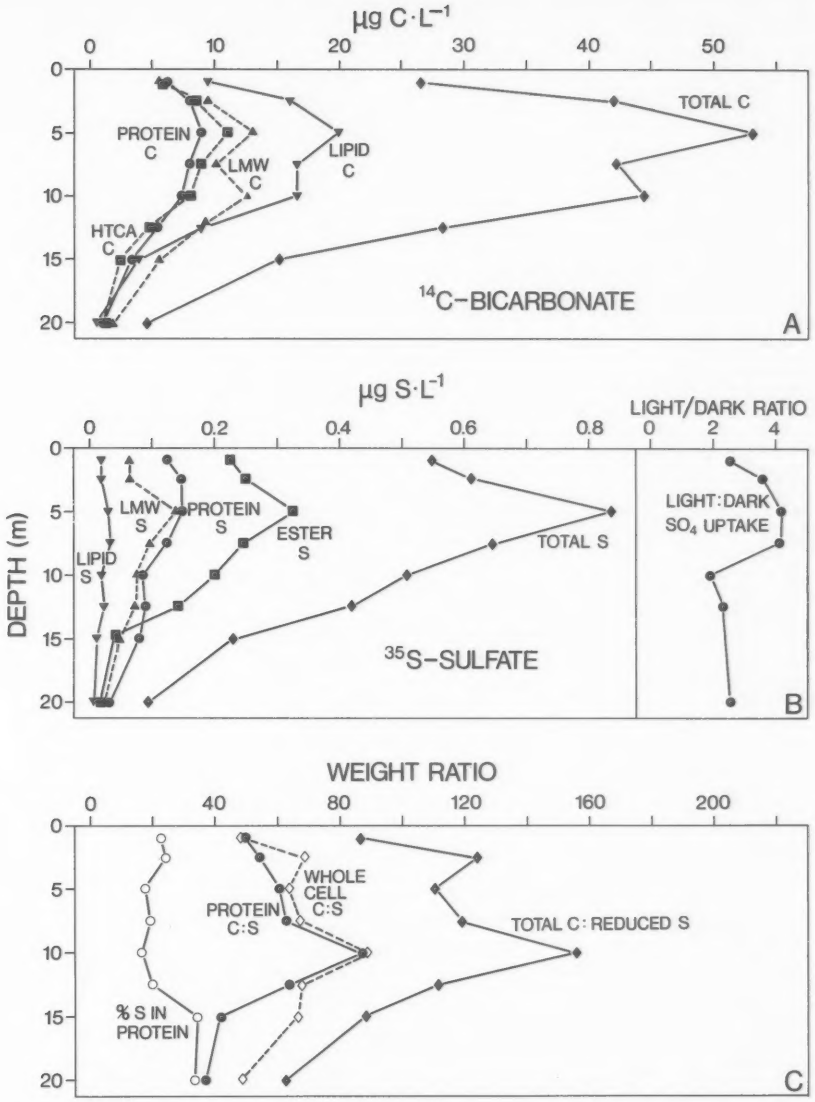

FIG. 3. Details of carbon dioxide and sulfate metabolism during all-day in situ incubation at station 401 on 8 June. (A) Carbon dioxide. (B) Sulfate; right-hand panel shows the light:dark sulfate uptake ratio. (C) C:S uptake ratios and proportion of total sulfur incorporated into protein.

5). Both protein C:S and total-C:reduced-S were lower than the June experiment and generally resembled the depth profile for photosynthesis.

Depth profiles of the light:dark sulfate uptake ratio displayed subsurface maxima at the depth of P_{max} in all cases (Table 3). Light stimulation of sulfate uptake increased markedly with incubation time, such that ratios from all-day incubations were generally two to three times the average for part-day samples. Quantitatively, summed dark sulfate uptake was about three times greater than the all-day rate, possibly reflecting enhanced algal dark uptake after previous light exposure. The midday dark uptake rates were almost twice those from the early morning sampling which had no prior light exposure. However, hourly dark sulfate uptake decreased to morning values in the late afternoon deployment. Light:dark ratios for $\%S_{ester}$ were >1 and for $\%S_{prot}$ were <1 only during the morning incubation (Table 2). These features were completely eliminated in later incubations but were again apparent in all-day samples.

All-day incubations may also yield systematically greater daily photosynthesis relative to summed part-day deployments, as shown for station 403 on 26 August. Although temperature was uniform in the upper 10 m (Table 1), there was a surface maximum in chlorophyll *a*. In turn, subsurface maxima in total carbon dioxide fixation occurred throughout the day, with an

TABLE 2. Protein and ester sulfate components of light (L) and dark (D) all-day in situ incubations at station 401 on 8 June 1982, with incubator data using 5-m water at station 401 on 9 June 1982 for comparison. N/A, not applicable.

Depth (m)	Total S, L:D	Ester sulfate			Protein S		
		Light	Dark	L:D	Light	Dark	L:D
		% of total ^{35}S in fraction					
1	N/A	41.1	43.7	0.94	22.8	21.3	1.07
5	N/A	39.0	24.6	1.59	17.9	24.7	0.72
12.5	N/A	34.0	17.8	1.91	20.3	31.9	0.64
20	N/A	15.9	5.0	3.18	33.8	62.9	0.54
5 m, P_{opt}	N/A	40.5	37.9	1.07	26.7	28.9	0.92
		ng $S \cdot L^{-1} \cdot d^{-1}$ in fraction					
1	2.55	225.5	93.9	2.40	124.9	45.8	2.73
5	4.19	325.9	49.1	6.64	149.3	49.3	3.03
12.5	2.33	142.1	31.9	4.45	84.9	57.1	1.49
20	2.55	14.8	1.8	8.22	31.6	23.1	1.37
5 m, P_{opt}	2.96	298.7	94.5	3.16	197.1	72.0	2.74

TABLE 3. Protein and ester sulfate components of light (L) and dark (D) all-day in situ incubations at station 403 on 26 August 1982, with incubator data using 5-m water at station 403 on 25 August 1982 for comparison. The depth of 1% I_0 was 10.8 m and received 7.9 μEinst. $\cdot m^{-2} \cdot s^{-1}$ at midday. N/A, not applicable.

Depth (m)	Total S, L:D	Ester sulfate			Protein S		
		Light	Dark	L:D	Light	Dark	L:D
		% of total ^{35}S in fraction					
1	N/A	25.2	31.0	0.81	32.0	39.0	0.82
5	N/A	25.0	31.9	0.78	35.2	39.9	0.88
12.5	N/A	21.2	35.9	0.59	43.5	39.1	1.11
20	N/A	46.8	52.0	0.90	51.6	44.9	1.15
5 m, P_{opt}	N/A	20.5	14.5	1.41	34.9	42.0	0.83
		ng $S \cdot L^{-1} \cdot d^{-1}$					
1	1.74	113.0	80.0	1.41	143.7	100.8	1.43
5	2.51	178.6	90.8	1.97	251.7	113.5	2.22
12.5	1.34	51.1	64.9	0.79	104.8	70.6	1.48
20	1.74	38.6	24.7	1.56	42.6	21.3	2.00
5 m, P_{opt}	3.67	125.8	24.2	5.20	214.3	70.4	3.04

extremely steep gradient during the midday incubation (Fig. 6). The pronounced midday depression of surface photosynthesis was accompanied by the only instance of a subsurface minimum in the $\%C_{prot}$ (Fig. 6).

As in the previous examples (Fig. 2 and 4), the amount of carbon fixed into protein was very similar between all-day and sum-of-parts incubations, with even smaller differences than for total carbon uptake (Fig. 6, bottom panel). Only the 1-m all-day incubation had lower protein-C as well as much lower total production. The small differences in protein carbon relative to total carbon fixation tended to accentuate a subsurface minimum in $\%C_{prot}$ for the all-day incubation. The isothermal composition of the upper 10 m combined with winds increasing to 20 knots on that day may have promoted sufficient mixing to prevent in situ photoinhibition at the surface (Putt et al. 1987) and hence enable greater photosynthesis in the 1-m afternoon sample.

Both total uptake and subcellular distribution of sulfur during the all-day incubation were well correlated with those for carbon (Fig. 7). The extent of surface depression in uptake was less pronounced for sulfur, resulting in a large increase in the cellular C:S ratios between 2.5 and 7.5 m. A slight increase in the light:dark sulfate uptake ratio was also found in this region. A similar, though muted trend was found for protein C:S ratios. The proportion of sulfur incorporated into protein increased below the depths of high productivity to slightly greater than 50% of the total sulfur assimilated in the deepest sample.

The three experiments described above demonstrate a very strong influence of time of day on the depth distribution and magnitude of photosynthesis measured by in situ techniques. Protein synthesis, measured by ^{14}C incorporation into protein, was much more uniform with depth than total carbon fixation, and this was supported by sulfur incorporation into protein in parallel incubations at station 405 (1 July 1982; Fig. 5). The smaller decrease in protein synthesis relative to total carbon fixation at photoinhibiting irradiance, documented during light intensity experiments (Cuhel and Lean 1987), was demonstrated for midday incubations during all three experiments.

Night Metabolism and Protein Synthesis in situ

Loss of previously fixed carbon during night respiration of algae is often a significant component of the total daily particulate organic carbon budget. A portion of the energy thus produced can be used for algal protein synthesis, leading to net assimilation of sulfate-S into protein accompanied by loss of carbon from energy storage reservoirs (e.g. LMW metabolites, polymeric carbohydrates, neutral lipids, etc.). Previously reported measurements from incubations in a light gradient implicated light history as a dominant factor controlling the extent of night metabolism (Morris 1981; Cuhel et al. 1984; Cuhel and Lean 1987). Overnight incubations during in situ productivity measurements provided corroborative data and reaffirmed the potential significance of night metabolism to nutrient flux and phytoplankton chemical composition. The following example, from the 26 August deployment at the central lake station, demonstrates several important processes associated with night algal growth.

All-day incorporation versus depth profiles for $H^{14}CO_3^-$ and $^{35}SO_4^{2-}$ (Fig. 7) included very strong subsurface assimilation maxima for both tracers, and this feature was also evident in the night component of carbon and sulfur metabolism. At 5 m, the depth of daytime P_{max}, total ^{14}C decreased by nearly 25% (Fig. 8). Respiration and redistribution of ^{14}C-labeled organic material reduced the polymeric carbohydrate (HTCA) and to a lesser extent LMW metabolite pools, but very little change in lipid-^{14}C was noted. Protein was the only fraction to increase in ^{14}C activity overnight. Net synthesis was confirmed by parallel incorporation of ^{35}S-labeled sulfate into protein, although sulfate was assimilated into cell components in proportions similar to daytime growth. No net loss of sulfur was observed during night incubation, and the subsurface peak of activity was much less pronounced than for carbon.

Night metabolism of in situ incubated plankton was far from trivial in Lake Ontario experiments. For the three experiments containing overnight components, one third to one half of the total daily protein synthesis occurred at night, based on the

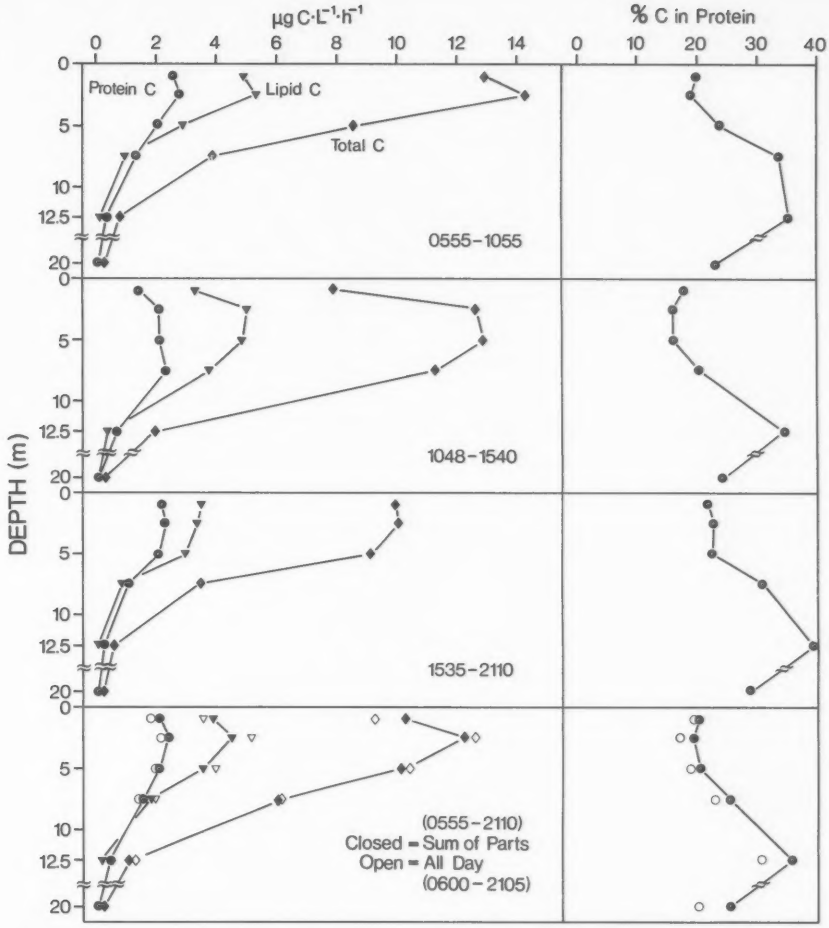

FIG. 4. Total carbon uptake and its incorporation into lipid and protein during back-to-back in situ incubations at station 405 on 1 July. The proportion of carbon incorporated into protein is shown in the right-hand panels. The bottom panels show the sum of the three incubations (solid symbols) compared with all-day (0600–2105) in situ incubation (open symbols).

assimilation of sulfur into the protein fraction (Table 4). The somewhat lower proportional increases of protein carbon reflect the varying specific activity of the newly incorporated ^{14}C in the different macromolecular fractions contributing to night protein synthesis. In general, 1 mg protein-^{14}C was incorporated at night for every 2–4 mg total ^{14}C respired or otherwise lost from the particulate matter (excretion was not measured). We stress the terms "mg ^{14}C," since the transformation of carbon among fractions and the environment occurs with a wide range of specific activities and hence need not reflect actual weight values for total particulate carbon. In contrast, ^{35}S is incorporated from exogenous supplies as needed and, with its small precursor pools, provides quantitative rates during both day and night incubations.

Discussion

Although long-term deployments for in situ carbon assimilation often result in lowered daily estimates of photosynthesis (Vollenweider and Nauwerek 1961; and others as reviewed in Harris 1978), from the results of the three detailed in situ experiments, it can be concluded that in Lake Ontario, all-day in situ deployments could be used as quantitative measurements of in situ primary productivity. Each represented a specific situation, i.e. thermal bar development, stratification during maximum phosphorus deficiency, and season's-end destratification. Total uptake and subcellular assimilation patterns of ^{14}C-labeled carbon were remarkably similar between all-day incubations and the sum of sequential deployments: considering the possible differences incurred in repetitive sampling of natural populations, the <25% "error" between the methods may be considered negligible. There was also similar agreement for ^{35}S-labeled sulfate in the example provided.

Within the particular experiments, however, there appeared several consistent features bearing on the primary productivity of the water masses themselves. The first of these involves photoinhibition of primary production by surface populations. It has been emphasized that retaining samples in bottles near the

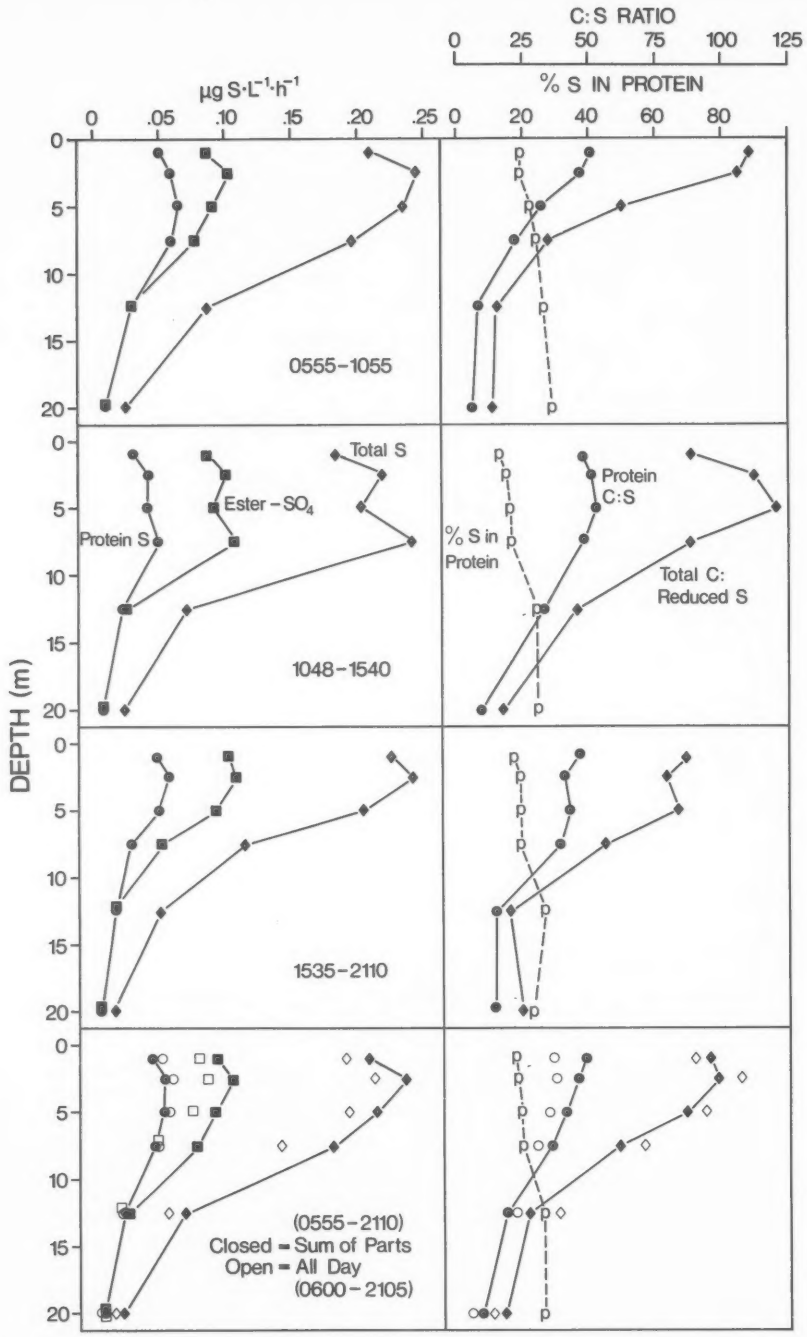

FIG. 5. Total uptake and incorporation of sulfur into protein and ester-SO_4^- during back-to-back in situ incubations at station 405 on 1 July. The proportion of sulfur incorporated into protein and C:S weight ratios for protein and total-C:reduced-S are shown in the right-hand panels. The bottom panels show the sum of the three incubations (solid symbols) compared with all-day (0600–2105) in situ incubation (open symbols).

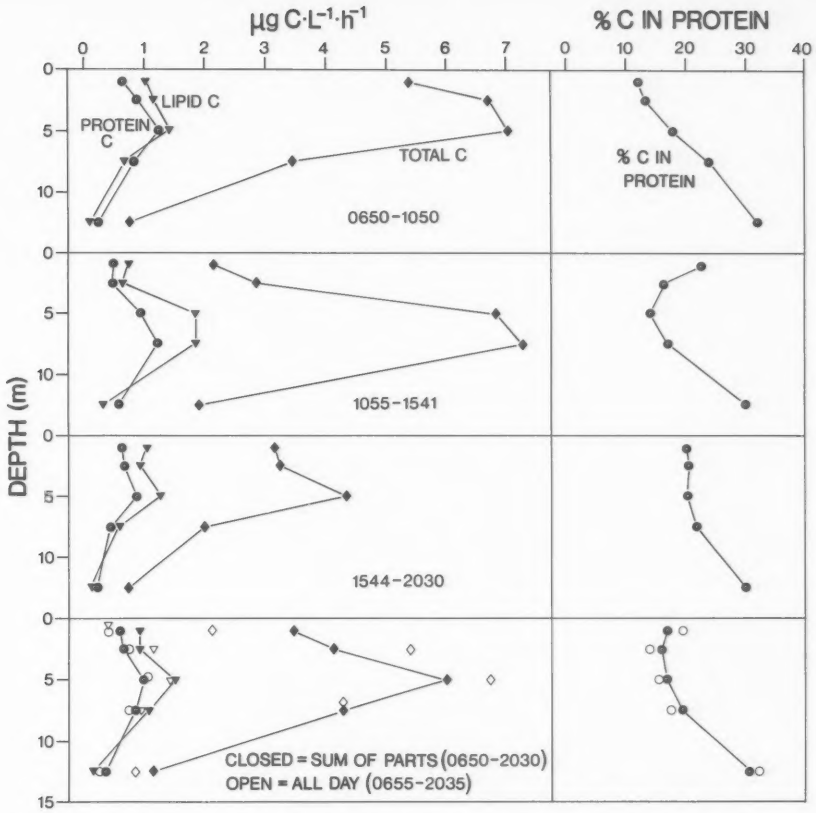

FIG. 6. Total carbon uptake and its incorporation into lipid and protein during back-to-back in situ incubations at station 403 on 26 August. The proportion of carbon incorporated into protein is shown in the right-hand panels. The bottom panels show the sum of the three incubations (solid symbols) compared with all-day (0655–2035) in situ incubation (open symbols).

surface prevents turbulent mixing through the water column experienced by unrestrained populations (cf. Marra 1978b). While this may well affect many measurements, cases may occur in which the mixed layer is sufficiently shallow that photoinhibiting irradiance exists throughout the mixed layer. Such an example may be found in the 8 June experiments (Fig. 2). The apparent depression of photosynthesis in surface samples during midday and afternoon incubations coincides with the only occasion in which an independent measure of photoinhibition, DCMU-enhanced fluorescence, also indicated in situ photoinhibition (Putt et al. 1987). In our other experiments, in situ photoinhibition may not have occurred: to assess the magnitude of error introduced by the in situ incubation, we have calculated the integrated daily production with and without photoinhibition (i.e. assuming that the chlorophyll *a* specific rate at the depth of P_{max} was maintained to the surface) (Table 5). In fact the greatest potential error was found on the day when DCMU-enhanced fluorescence suggested the occurrence of in situ photoinhibition. Overall, however, error due to this factor was much less than 10% for full-day productivity estimation.

Vertical heterogeneity in the compositon of the plankton population was well demonstrated in the 8 June experiment at station 401. Because longshore current velocities were highly variable (Simons and Schertzer 1987), sequential sampling points at a given depth did not necessarily contain similar populations. Vertical gradients in production characteristics were also encountered and were expressed most clearly in the subcellular distribution of incorporated tracers. While deeper samples were exposed to lower light fluxes, the variability in percent ester sulfate (Table 2) with depth was much greater than could be attributed to light intensity effects alone, based on an incubator experiment at the same station the next day. In fact, very little light effect was demonstrated for the proportion of sulfur entering this product in the homogeneous population of the light intensity experiment, as found for the 1-m in situ sample.

The magnitude of increase in the proportion of protein-S with depth (Table 2) was also much greater than the weak effects of light intensity alone (Cuhel and Lean 1987). The proportion of sulfur in bacterial protein is considerably larger (usually >70%) than for algae (Cuhel et al. 1984): the maximum of 63% at 20 m is reminiscent of typical bacterial sulfur distribution (Cuhel et al. 1982) suggesting increased heterotrophic activity relative to phytoplankton in the deepest samples. Further evidence for bacterial activity was found in comparison of the subcellular distribution of sulfur in light- and dark-incubated samples.

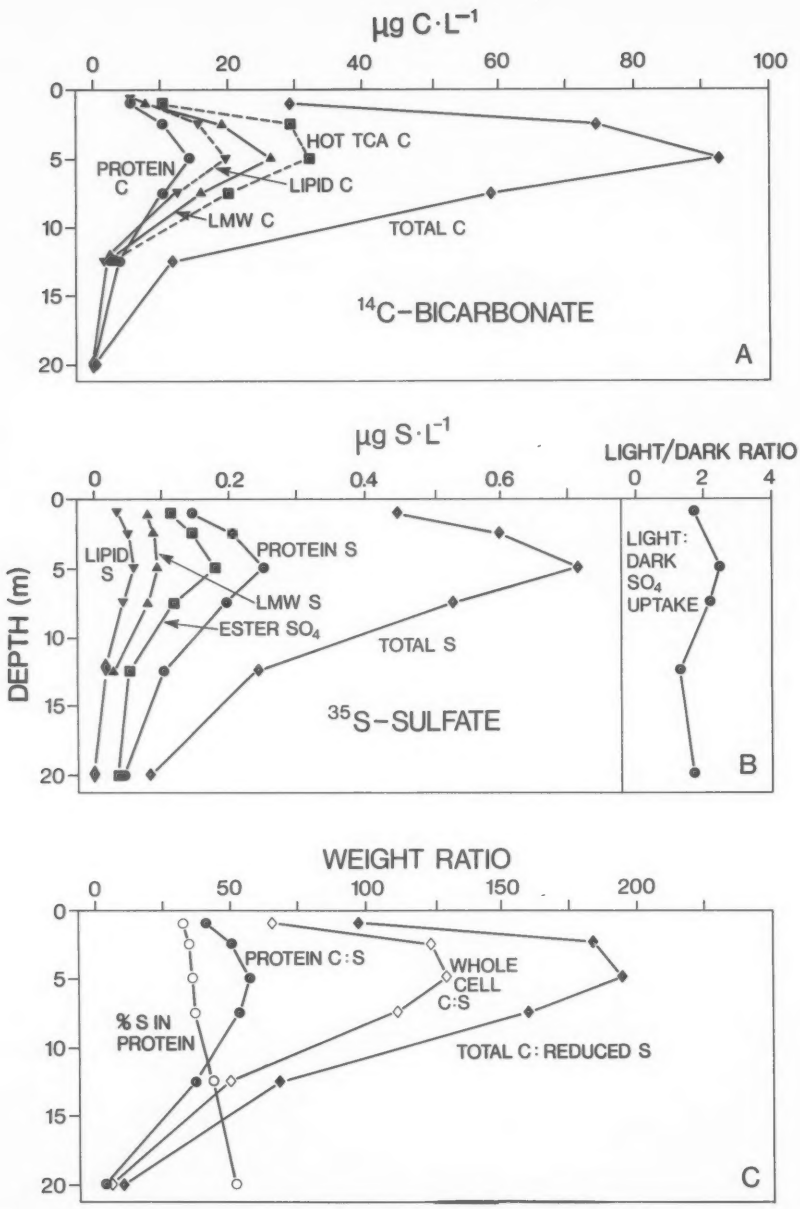

FIG. 7. Details of carbon dioxide and sulfate metabolism during all-day in situ incubation at station 405 on 26 August. (A) Carbon dioxide. (B) Sulfate; right-hand panel shows the light:dark sulfate uptake ratio. (C) C:S uptake ratios and proportion of total sulfur incorporated into protein.

Algal protein turnover in the absence of net synthesis results in ^{14}C incorporation into protein but not of ^{35}S (Cuhel et al. 1984). Hence, the unusually high protein C:S ratios in the upper water column may be indicative of substantial algal protein turnover, but this conclusion remains tentative. Further work is necessary to clarify the meaning of the C:S ratio when applied to mixed microbial populations.

During the 1982 Lake Ontario Nutrient Assessment Study (LONAS), six all-day in situ measurements of carbon and sulfur metabolism were conducted, three at inshore stations (401 and 405) and three at the central lake station (403). Depth profiles for temperature, chlorophyll *a*, assimilation number, and the percent carbon or sulfur incorporated into protein are shown in Fig. 9 and 10 (inshore and central lake stations, respectively). Maximum assimilation numbers (grams carbon per gram chlorophyll *a* per hour) were 1.1–1.5 (inshore) and 0.9–2.2

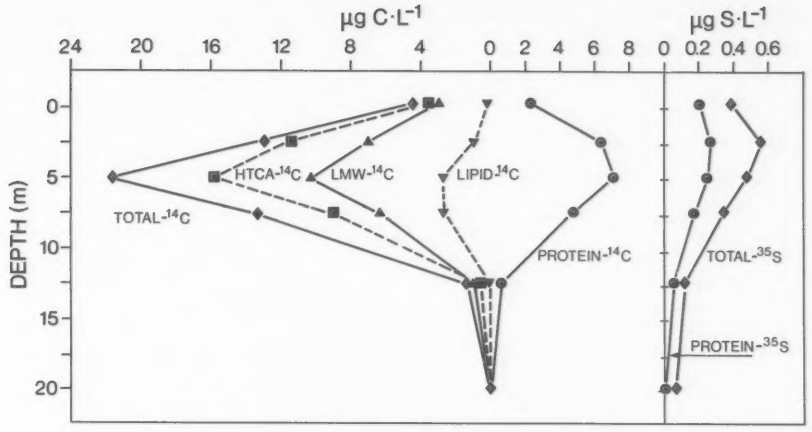

FIG. 8. Night changes in total carbon and sulfur and their subcellular components for station 403 on 26 August. Natural photoperiod 13.5 L : 10.5 D. Note: amounts are calculated for the specific activity of the *initial inorganic* ^{14}C and hence underestimate fluxes out of macromolecular components.

TABLE 4. Light day, night, and 24-h integrated particulate production for stations with overnight in situ deployments. Night values are the difference between light day and 24-h measurements.

		Particulate production ($mg \cdot m^{-2}$)					
		Carbon		Sulfur			
Date/station	Photoperiod	Total	Protein	Total	Reduced	Oxidized	Protein
29 June,	15.5 L	1080.2	194.6	21.5	12.9	8.6	5.8
station 401	8.5 D	−124.1	+96.9	12.7	9.5	3.2	4.9
	24 h	956.1	291.5	34.2	22.4	11.8	10.7
26 August,	13.6 L	713.8	127.9	7.5	5.1	2.4	2.8
station 403	10.4 D	−143.7	+54.3	5.2	3.9	1.3	2.5
	24 h	570.1	182.2	12.7	9.0	3.7	5.3
22 September,	12.2 L	890.6	136.8	13.0	11.1	1.9	2.1
station 403	11.8 D	−144.2	+30.3	1.0	0.8	0.2	1.1
	24 h	746.4	167.1	14.0	11.9	2.1	3.2

(offshore), significantly lower than the 1.1–4.5 and 1.6–5.7 reported by Glooschenko et al. (1974) and Stadelmann et al. (1974) for similar Lake Ontario stations during the International Field Year of the Great Lakes (IFYGL). In most cases, subsurface maxima for assimilation number coincided with minima in percent carbon incorporated into protein, but no relationship was found between assimilation number and percent sulfur in protein. This is consistent with the lack of light intensity effect on patterns of sulfur metabolism in general (Cuhel and Lean 1987).

Even though photosynthetic efficiency and soluble reactive phosphorus (Stevens et al. 1987) were markedly lower in the lake, June–September integrated areal production estimates (0.6–1.5 g $C \cdot m^{-2} \cdot d^{-1}$) were in good agreement with those of Stadelmann et al. (1974) (0.3–1.9 g $C \cdot m^{-2} \cdot d^{-1}$).

Integrated carbon fixation to sulfate reduction ratios averaged 99 by weight, a value similar to the *composition* of microorganisms in general (Jordan and Peterson 1978; Cuhel et al. 1984; Cuhel and Waterbury 1984), but not necessarily to short-term uptake (Monheimer 1978a). Nonreductive sulfate assimilation processes, particularly ester sulfate formation, were often more than 30% of total sulfur assimilation and can contribute significantly to sediment sulfur cycles as electron sinks for the oxidation of organic matter. In fact, our estimates of sulfate ester formation (Table 4), 2–12 mg $S \cdot m^{-2} \cdot d^{-1}$, are consistent with observed rates of reduction of organic sulfate esters in lake sediments (approximately 3 mg $S \cdot m^{-2} \cdot d^{-1}$) reported by Smith and Klug (1981).

Night metabolism of algae can include biosynthesis of protein and nucleic acids at rates equal to daytime growth (cf. Cuhel et al. 1984). For photosynthetic organisms this capability has substantial physiological significance, as it represents complete uncoupling between carbon and energy accumulation and utilization. The temptation to consider relative night growth of algae as an index of nutrient deficiency (Lancelot and Mathot 1985) must be yielded to cautiously, however. Since daylength varies considerably in higher latitudes, relative amounts of products must be interpreted in terms of their respective rates;

TABLE 5. All-day in situ production integrated 0–20 m with (+) and without (−) photoinhibition (PI). Integrations without photoinhibition assume uniform chlorophyll *a* specific photosynthesis from the depth of P_{max} to the surface. No photoinhibition was apparent on 29 June (station 401) or 26 August (station 403). N/A, not available.

		Carbon		Sulfur		
Date/station	PI	Total	Protein	Total	Reduced	Protein
8 June,	+	616.2	116.3	9.26	5.48	1.99
station 401	−	690.3	124.1	10.23	6.08	2.05
	% diff.	12.0	6.7	10.5	10.9	3.0
10 June,	+	552.6	40.4	N/A	N/A	N/A
station 403	−	565.4	43.0	N/A	N/A	N/A
	% diff.	2.3	6.4			
1 July,	+	1467.2	299.1	32.38	19.03	9.80
station 405	−	1573.0	309.3	33.11	19.50	10.05
	% diff.	7.2	3.4	2.3	2.5	2.6
22 September,	+	890.6	136.8	13.03	11.13	2.13
station 403	−	912.9	141.1	13.12	11.18	2.16
	% diff.	2.5	3.1	0.7	0.4	1.4
	Avg. diff.	6.0	4.9	4.5	4.6	2.3

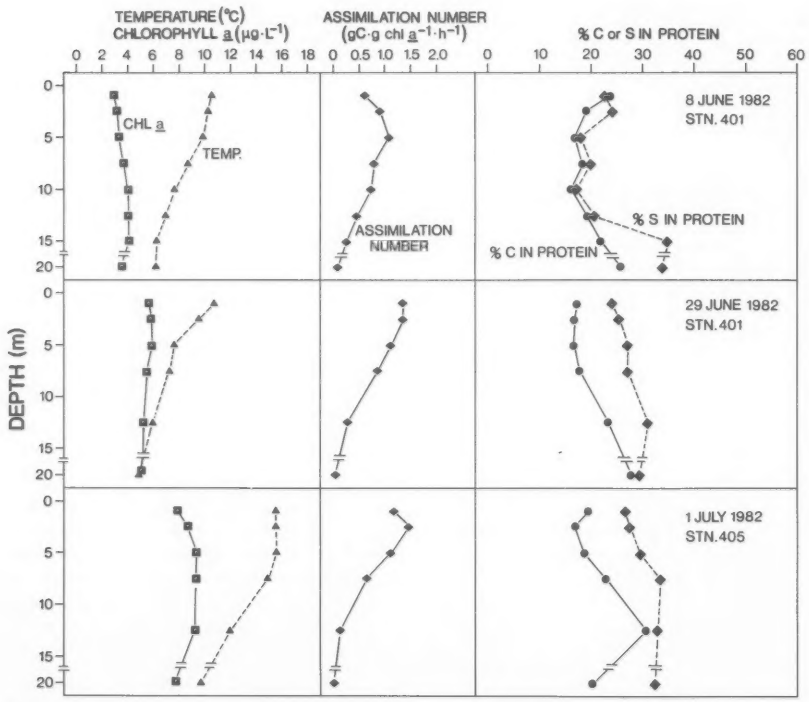

FIG. 9. Vertical profiles for temperature, chlorophyll *a*, assimilation number, and the percentage of total assimilated C or S in protein for all-day in situ incubations at inshore stations during LONAS, 1982. Daily integrated production is given in Tables 4 and 5.

otherwise, night metabolism will appear inconsequential when nights are short. More difficult considerations include isotopic equilibration artifacts, discussed below and in Cuhel and Lean (1987), as well as the nonubiquity of night protein synthesis capability among algae.

Two consequences of night synthesis are a net increase in certain biochemical constituents (e.g. protein) and a continued demand for nutrients. The energy used for night synthesis is derived from carbohydrates, generally requiring degradation of polymeric carbohydrates stored during daylight hours. Therefore, elemental ratios such as C:N and C:S and cell composition ratios such as protein:carbohydrate and protein:lipid may sys-

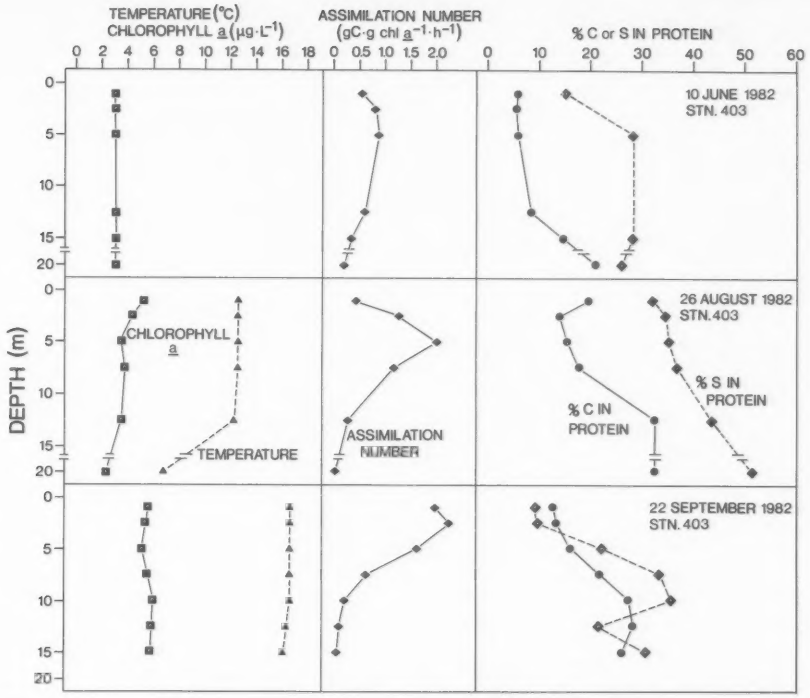

FIG. 10. Vertical profiles for temperature, chlorophyll *a*, assimilation number, and the percentage of total assimilated C or S in protein for all-day in situ incubations at the central lake station during LONAS, 1982. Both temperature and chlorophyll *a* were uniform with depth at 3 units on 10 June (upper panels). Daily integrated production is given in Tables 4 and 5.

TABLE 6. Euphotic zone doubling times for total particulate organic carbon and protein based on integrated light day or 24-h in situ measurements and integrated standing stocks of POC and protein. Protein data are from Pick (1987). A protein composition of 52.6% C and 1.1% S is used (Jukes et al. 1975).

Date/station	Incubation period	Days to double standing stock		
		POC (^{14}C)	Protein (^{14}C)	Protein (^{35}S)
29 June,	Light day	9.2	19.4	13.6
station 401	24 h	10.4	13.0	7.4
26 August,	Light day	10.8	22.0	21.1
station 403	24 h	13.6	15.5	11.1
22 September,	Light day	11.0	18.1	24.7
station 403	24 h	13.1	14.9	15.7

tematically change throughout the night. Combined ^{14}C-labeled bicarbonate and ^{35}S-labeled sulfate assimilation studies carried out overnight can describe night synthesis unambiguously.

Several of the in situ experiments included an overnight component for which the data of 26 August (station 403) will serve as an example (Fig. 8). The flow of carbon was primarily into protein from carbohydrates, with all activity mediated by the LMW fraction (through which polymeric carbohydrate degradation products are transformed). The energetic costs of night protein synthesis include at least 5 ATP for each peptide bond formed plus 17–18 ATP for each reductively assimilated SO_4 molecule (1 every 30 amino acids) in addition to the transformation of carbon skeletons, transamination reactions, etc. These costs are met through oxidative metabolism of carbohydrates. Thus, one carbon unit is incorporated into protein for every three to five units removed from the (LMW + polymeric) carbohydrates: the flow of carbon into protein was accompanied by a similar assimilation of exogenous sulfate into protein. One result of these activities is a dramatic alteration in the ratios of ^{14}C-labeled biopolymers to one another (Fig. 11). While incorporation patterns from all-day incubation yielded quite variable ratios with dominance of carbohydrates in evidence, overnight incubation and associated night growth returned the relative abundance of the major biopolymers to near unity in the upper water column (lower panel). Such uniform relative abundance has been suggested to be optimal food quality for some herbivores (cf. Scott 1980).

For the observed redistribution of carbon to actually have a noticeable effect on the food quality of plankton requires that the bulk composition of the plankton change in kind overnight. That is, the composition of the total particulate carbon must be altered appreciably. It is not sufficient that the recently assimilated and hence ^{14}C-labeled component of the particulate material undergo these changes if it accounts for a small fraction of the total particulate carbon. We have therefore considered the approximate doubling time of the plankton population with respect to total particulate carbon and the protein component specifically. Using integrated production values from Table 4 and integrated particulate organic carbon and particulate protein

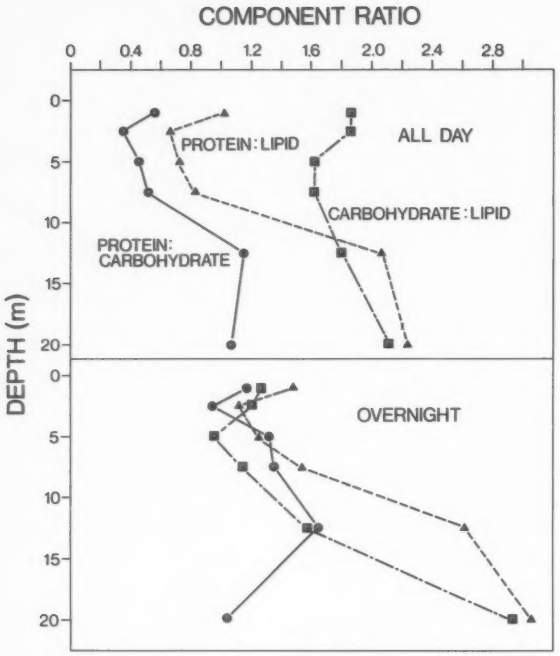

FIG. 11. Ratios of major ^{14}C-labeled biopolymers following all-day and overnight in situ incubation at station 403 on 26 August.

(Pick 1987), we estimated the days required to double either the particulate organic carbon or protein stocks using either light day or 24-h production measurements (considering each as a "day" for calculation purposes; Table 6). The significance of night metabolism is accentuated in these calculations: since protein synthesis at night is energized by oxidative carbon metabolism, full 24-h growth measurements indicate faster protein-specific and slower carbon-specific growth rates than the light day estimates. Three stations with 24-h measurements had average particulate organic carbon and protein increases of 9.7 and 6.0% $\cdot d^{-1}$ using light day data but 8.2 and 10.6% based on 24-h incubations. In light of these findings, the diel vertical migration of herbivores (Taylor et al. 1987) may be related to food quality, but other factors may be involved in Lake Ontario where the growth rate of the particulate material was too slow for a single day's night metabolism to significantly alter the biochemical community structure.

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Influence of Light Intensity, Light Quality, Temperature, and Daylength on Uptake and Assimilation of Carbon Dioxide and Sulfate by Lake Plankton

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The biochemical composition of newly produced phytoplankton biomass in Lake Ontario varied systematically with respect to experimentally manipulated incident light intensity and environmentally imposed water temperature and daylength, but was insensitive to light quality. Total uptake of ^{14}C-labeled bicarbonate was light dependent (P_{opt}:dark = 60–200), while $^{35}SO_4^{2-}$ uptake was light stimulated (P_{opt}:dark < 5). Subcellular allocation of ^{14}C for relative protein, carbohydrate, and lipid polymer synthesis responded sensitively to subsaturating light. Pathways of ^{35}S assimilation were unaffected by light intensity. Night protein synthesis and attendant respiration of polymeric carbohydrates was a function of prior light history: with daytime illumination at P_{opt}, day and night rates of $^{35}SO_4$-S incorporation into protein were often indistinguishable. Using April–November data from P_{opt} only, allocation of carbon to carbohydrate polymer storage for night growth was strictly proportional to nightlength. The proportion of carbon contained in protein was strongly correlated with in situ water temperature. The lack of cross-correlation suggests that temperature and daylength exert independent constraints on the biochemical composition of lake microplankton.

La composition biochimique de la biomasse phytoplanctonique récemment produite dans le lac Ontario a varié de façon systématique par rapport à l'intensité de la lumière incidente manipulée expérimentalement et à la température de l'eau et à la longueur du jour imposées au milieu, mais n'a pas réagi à la qualité de la lumière. L'absorption totale de bicarbonate ^{14}C était fonction de la lumière (P_{opt}:obscurité = 60–200) tandis que l'absorption de $^{35}SO_4^{-2}$ était accentuée par la lumière (P_{opt}:obscurité < 5). La répartition subcellulaire de ^{14}C en ce qui concerne la synthèse relative de protéines, d'hydrates de carbone et de polymères lipidiques a réagi positivement à une lumière en-dessous du point de saturation. Les voies d'assimilation du ^{35}S n'ont pas été affectées par l'intensité de la lumière. La synthèse des protéines pendant la nuit et la respiration concomitante d'hydrates de carbone polymérisés étaient fonction du régime d'éclairement antérieur: avec une illumination pendant la journée à P_{opt}, les taux d'incorporation de $^{35}SO_4$-S dans la protéine pendant le jour et la nuit étaient souvent indiscernables. En utilisant les données de P_{opt} seulement d'avril à novembre, l'affectation du carbone pour entreposage sous forme de polymères d'hydrates de carbone servant à la croissance pendant la nuit était strictement proportionnelle à la longueur de la nuit. On a établi une forte corrélation entre la proportion de carbone contenu dans les protéines et la température de l'eau *in situ*. Le manque de corrélation croisée donne à penser que la température et la longueur du jour exercent des contraintes indépendantes sur la composition biochimique du microplancton du lac.

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Photoautotrophic assimilation of nutrients and generation of energy for biosynthesis often may be limited by the availability of photosynthetically active radiation. Photosynthetic activity responds predictably to variations of instantaneous intensity, total daily flux, daylength, and spectral distribution; each may impose limits upon total daily carbon fixation and/or macromolecular products of photosynthesis by natural populations.

Few freshwater studies have examined what fraction of total carbon fixed goes to reproductive growth (i.e. biosynthesis of the complete suite of macromolecules required to promote cell division) relative to synthesis of storage products. While the literature on quantitative relationships between light intensity and photosynthesis is copious, little attention has been paid to specific end products of photosynthetic carbon fixation in freshwater algae. In freshwater ecosystems this approach has been applied only to the study of Cyanobacteria (cf. Konopka and Schnur 1980). The relative flow of fixed carbon into specific macromolecular end products (e.g. lipid, carbohydrate, protein) may serve as an independent means of assessing the

nutritional status of the phytoplankton (Bates 1981; Morris et al. 1974). Biochemical composition studies may additionally provide information on algal nutritional value as food for herbivores (c.f. Scott 1980).

Several hypotheses have been drawn from culture and field work on light intensity modulation of photosynthetic products in marine phytoplankton which may also be applicable to freshwater studies. Morris et al. (1974) have shown that the proportion of ^{14}C-labeled bicarbonate incorporated into protein is often inversely proportional to light intensity. This suggests that subsaturating light favors protein synthesis rather than storage of carbohydrates. They have used these results to explain observations of an increase in the proportion of protein-^{14}C with depth of incubation in the euphotic zone of coastal and open ocean environments.

Unfortunately, it cannot be assumed that the amount of $^{14}CO_2$-C entering specific biochemical compartments is always quantitatively related to their net biosynthesis. Although the pools of low molecular weight (LMW) metabolites reach isotopic equilibrium with the added tracer rapidly enough in light incubations of growing populations (Cuhel and Waterbury 1984; Lancelot and Mathot 1985; but see also Di Tullio and Laws 1983), turnover of macromolecules or use of polymeric carbon reserves during night metabolism can alter the specific activity of the cellular ^{14}C incorporated into new products. The magnitude of potential interference is not readily detectable with $^{14}CO_2$ assimilation studies alone.

Sulfate is an essential nutrient for microbial growth, being required for protein synthesis and photosynthetic electron transport systems, yet measurement of its assimilation into microbial biomass is not hampered by several of the problems common to phosphorus and nitrogen uptake studies (Cuhel et al. 1982). Sulfate is so abundant in aquatic systems that substrate depletion during incubation never occurs (typical uptake rates of added ^{35}S-labeled sulfate are $<0.001\% \cdot h^{-1}$). As a result, there is no need for microorganisms to store sulfur in excess of immediate growth requirements. Incorporation of sulfate into protein therefore provides a rate measurement of protein synthesis which is useful in comparison with subcellular redistribution of ^{14}C from bicarbonate for investigation of night protein synthesis (Cuhel et al. 1984).

The influences of light intensity and incubation time are important factors controlling the total amount and biochemical incorporation patterns of CO_2-C and SO_4-S (Cuhel and Lean 1987). Superimposed on incubation time is the effect of "local time" relative to the day/night cycle as well as the presence or absence of light itself. Metabolism and growth of algae at night has been frequently overlooked in both laboratory and field studies, despite a developing literature stressing the widespread occurrence of cell division periodicity cued to day/night cycles (cf. Brand and Guillard 1981; Jorgensen 1966; Weiler and Eppley 1979; reviewed by Chisholm 1981).

The spectral distribution of solar radiation differs markedly from that of light at various depths in the water column due to selective extinction by the water itself and through absorption by dissolved organic matter and photosynthetic pigments. This difference is one of the reasons used to promote in situ rather than incubator measurements of primary productivity. Surprisingly little is known about the actual influence of light quality on quantitative aspects of phytoplankton photosynthesis and macromolecular synthesis. Major contributions by Wallen and Geen (1971a, 1971b) documented stimulation of protein synthesis by blue and green light in pure cultures of algae. Synthesis of tricarboxylic acid cycle-related amino acids (Asp, Glu) is stimulated by as little as 5 min of exposure to blue light (Hauschild et al. 1962) and is enhanced threefold over white light in only 30 min. Field measurements of nearly unialgal populations of colonial chrysophytes often found at metalimnetic chlorophyll maxima also demonstrated green light stimulation of protein synthesis (Pick and Cuhel 1986). Algae in nature grow under variable wavelength–distribution conditions, and their pattern of carbon incorporation into macromolecules may reflect enhanced photosynthesis and action spectrum shifts due to auxiliary pigments. An experiment was therefore conducted to ascertain the magnitude of light quality effects which might lead to differences in results from controlled light and in situ productivity studies.

Our diel studies of $^{14}CO_2$-C and $^{35}SO_4$-S incorporation as a function of light intensity were designed to (1) test the similarity of freshwater and marine phytoplankton light intensity dependent macromolecular synthetic patterns, (2) document the influence of light intensity on sulfate assimilation, (3) provide collaborating data for the in situ experiments to assess the proportion of carbon fixation variability attributable to light intensity alone, and (4) establish the dependence of night protein synthesis on prior light intensity history. The experiments spanned diel light cycles from 10 L:14 D to 16 L:8 D and temperatures from 1.2 to 18.7°C; thus, we were able to document several seasonal trends for which light intensity effects may have been secondary to other factors.

Materials and Methods

The transmission spectra for incident light, near-surface, and deeper euphotic zone water, unfiltered white light from the primary incubator used for light intensity experiments, and a second incubator used for the control samples are compared in Fig. 1. For the light quality experiment, incoming light was modified with red, blue, or green color filters (Fig. 1D). The light from the control incubator closely resembles incident radiation and near-surface water whereas the experimental incubator provides light resembling that found between about 5 and 15 m. The only serious trough in the spectrum from the experimental incubator (500–520 nm) fortuitously occurs at the absorption minimum for chlorophylls *a*, *b*, and *c* and is well below the approximately 550-nm absorption maximum of phycobiliproteins (O'Carra and O'h Eocha 1976). Fucoxanthin, a principal accessory pigment in diatoms, does have maximum absorbance just above 500 nm (Jorgensen 1977), but the very broad absorption maximum of this pigment imparts good light harvesting capability at the wavelength of maximum output in the incubator. Thus, selective elimination of photosynthesis by groups of algae containing specific pigments is not likely. Each of the color filters effectively restricted the range of output wavelengths. The spectral distribution of light from the different sources was measured with a LiCor QSM 1-2500 quantum spectrometer; light flux in the photosynthetically active 400–700 nm waveband was measured with a LiCor LI-185A quantum meter.

Water samples were collected before dawn in 5-L Niskin bottles, usually at a depth of 5 m, pooled in a 20-L carboy, and dispensed into 300-mL glass BOD bottles. Replicate bottles, enough to provide for two isotopes at five to six light intensities plus zero time blanks, were inoculated with either ^{14}C-labeled bicarbonate (2 $GBq \cdot mmol^{-1}$, 20 $dpm \cdot ng\ C^{-1}$ final specific activity) or ^{35}S-labeled sulfate (carrier free, 150 $dpm \cdot ng\ S^{-1}$

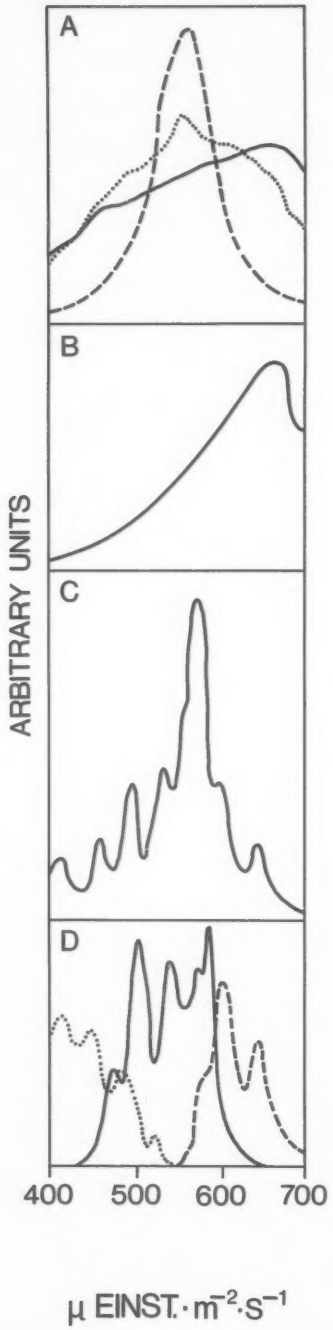

FIG. 1. Wavelength distribution of natural and artificial light relevant to the light quality experiment. (A) Incident sunlight (solid line) and solar radiation at 2 m (dotted line) and 10 m (broken line); (B) artificial light in the incubator used for controls; (C) artificial light in the experimental incubator without filters; (D) as for Fig. 1C but with blue (dotted line), green (solid line), or red (broken line) filters.

TABLE 1. Hourly ^{14}C-labelled bicarbonate fixation rates and percentage of total fixed carbon in protein and lipid for white light controls. The normalization factor for each incubation was the ratio of the mean for all incubations to the average of duplicate bottles for each incubation.

Experiment	$\mu gC \cdot L^{-1} \cdot h^{-1}$	Correction factor	% total ^{14}C in: Lipid	Protein
Red				
A	9.183		23.9	19.9
B	8.838		23.9	18.4
Average	9.011	0.912	23.9	19.2
Blue				
A	8.359		29.7	24.2
B	8.713		28.6	24.7
Average	8.536	0.963	29.2	24.5
Green				
A	7.733		27.5	20.8
B	7.749		26.3	20.1
Average	7.741	1.068	26.9	20.5
White				
A	7.534		25.7	16.8
B	7.641		27.4	15.8
Average	7.588	1.083	26.6	16.3
Mean	8.219		26.6	20.1
SD	0.637		2.1	3.2
C.V. (%)	7.8		7.9	15.9

final specific activity) and the bottles placed on a rotating wheel in one of two temperature- and light-controlled incubators. The light cycle was coincident with local apparent sunrise and sunset. Filtration methods and subcellular fractionation procedures used to separate LMW, alcohol-soluble protein, lipids, hot trichloroacetic acid (HTCA) soluble material, and residue protein are detailed in the accompanying in situ paper (Cuhel and Lean 1987).

Water for the light quality experiment was collected from 7.5 m at 2.5- to 3-h intervals at midlake station 403 and dispensed into steam-cleaned 300-mL BOD bottles. Replicate bottles were inoculated with ^{14}C-labeled bicarbonate (final specific activity 17 $dpm \cdot ng\ C^{-1}$) and placed in the principal incubator. Freshly collected water samples were used for each color to minimize dark containment-induced changes in macromolecular synthesis; therefore, duplicate reference samples were also incubated at saturating white light in a second incubator at the same temperature. After 2–3 h, the bottles were removed and 100-mL subsamples filtered through Whatman GF/F filters. One of the samples was processed by the subcellular fractionation procedure previously described for this study; the remaining samples were counted whole. Overall, both internal and external duplicates agreed well, with average error under 7%.

To provide quantitative comparison of photosynthetic rates with plankton samples collected at different times, we normalized all uptake data to a constant hourly rate for the control samples in the second incubator. The mean rate shown in Table 1 was used to determine the normalization factor for the individual incubations; all factors were $<10\%$. The agreement of subcellular ^{14}C distribution among incubations was sufficient

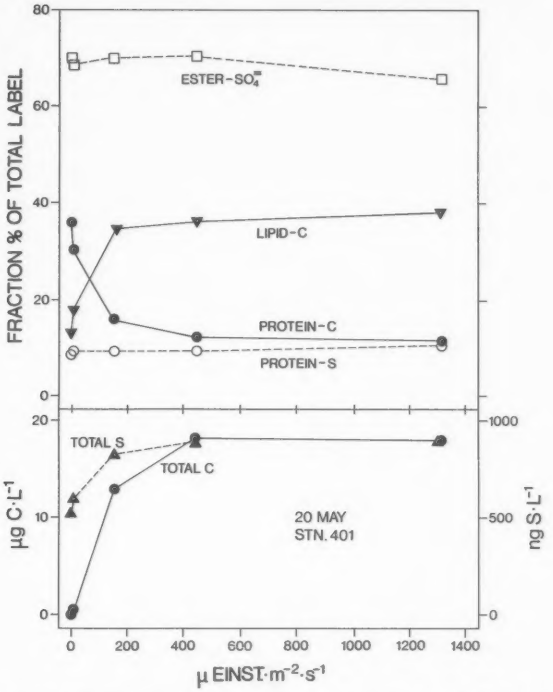

FIG. 2. Light intensity stimulation of short-term (3.2 h) $^{14}CO_2$-C and $^{35}SO_4$-S uptake (lower panel) and proportional incorporation into selected macromolecular components (upper panel) for station 401 on 20 May.

to distinguish differences of about 2% within an incubation and about 5% between incubations.

Results

Macromolecular Incorporation Patterns of Carbon and Sulfur

Several features common to all light gradient experiments are illustrated in Fig. 2 for the inshore station 401 on 20 May. Uptake of ^{14}C-labeled bicarbonate and ^{35}S-labeled sulfate was light saturable, but sulfate uptake approached saturation at an intensity significantly less than that required for maximal carbon dioxide fixation. The characteristic decreasing proportion of carbon incorporated into protein with increasing light intensity (summarized by Morris (1980)) offset by increasing proportional lipid incorporation is clearly distinguishable from the light intensity independent assimilation pattern of sulfate. At this station early in the season, the dominance of diatoms (Gray 1987) is reflected in the very high proportion of sulfate esters, which account for 70% of the total sulfur fixed in this example. High diatom productivity and associated nonreductive ester-SO_4^{2-} synthesis was marked by very low whole-cell ^{14}C:^{35}S uptake ratios (~20), while total ^{14}C:reduced-^{35}S values remained typical of microbial biomass (~70).

Light Quality

While chromatic adaptation is of advantage to populations residing for prolonged periods in subsurface waters, plankton of the mixed layer may not experience restricted light fields long enough to induce physiological response (Falkowski 1984). Hence, the lack of consistent effect of light quality on total carbon dioxide fixation (Fig. 3A) of midsummer epilimnetic phytoplankton was not unexpected. Both blue and red light yielded reduced total photosynthesis at intermediate intensities (~200 µEinst.·m^{-2}·s^{-1}), but initial slopes and final apparent maximum photosynthetic rates were similar for all colors. At the highest light intensities, deviation from the rate in white light was less than 15% for red light (enhancing) and blue light (inhibiting).

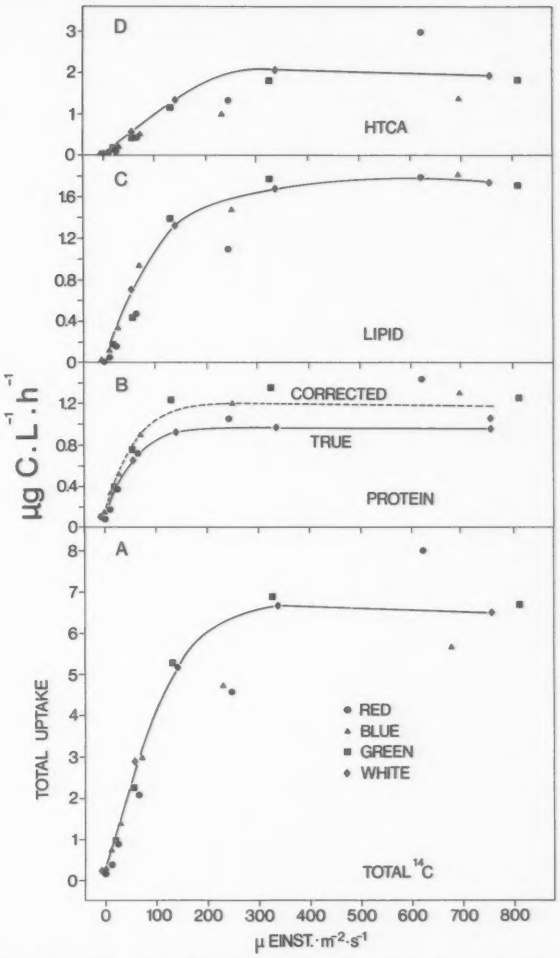

FIG. 3. (A) Total uptake and incorporation of $^{14}CO_2$-C into the (B) protein, (C) lipid, and (D) carbohydrate components of Lake Ontario plankton under red, blue, green, and white light.

The amount of $^{14}CO_2$-C incorporated into protein, lipid, and HTCA-soluble material increased similarly with light intensity for the different experiments (Fig. 3B, 3C, 3D). The white light control experiment, conducted on a very late afternoon sample, had a lower percentage incorporation of ^{14}C into protein than the standards from the second incubator for the color experiments (Table 1); the broken line in Fig. 3B denotes the rate corrected

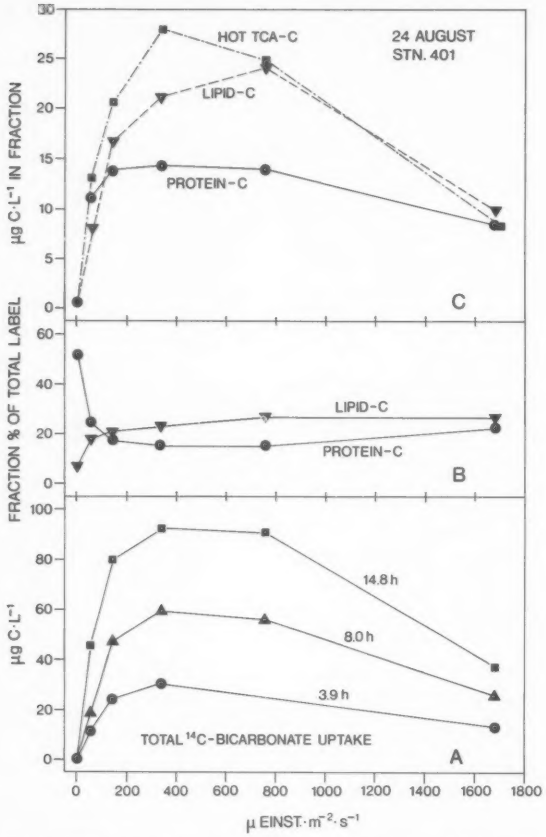

FIG. 4. $^{14}CO_2$-C uptake and metabolism as a function of light intensity for station 401 on 24 August. (A) Time course of total ^{14}C fixation; (B) proportion of total fixed ^{14}C in protein and lipid after 14.8 h; (C) amount of ^{14}C fixed into protein, lipid, and HTCA-soluble material after 14.8 h.

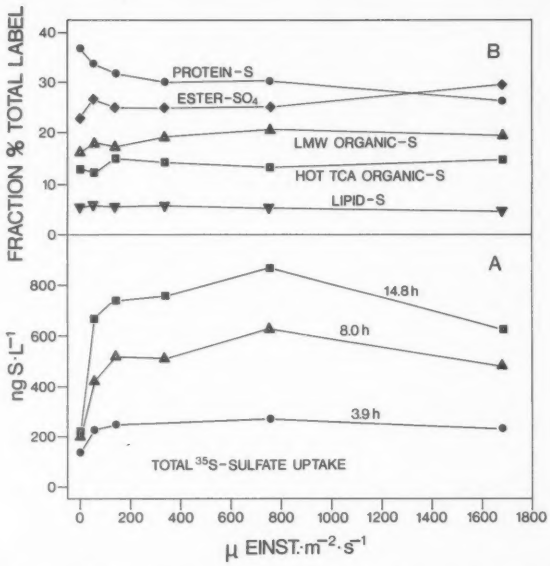

FIG. 5. $^{35}SO_4$-S uptake and metabolism as a function of light intensity for station 401 on 24 August. (A) Time course of total ^{35}S assimilation; (B) proportional distribution of fixed ^{35}S after 14.8 h.

for the mean protein synthesis of all the white controls. Even without this consideration, there was but a small enhancement of ^{14}C incorporation into protein in colored light. No distinguishable differences were found for either lipid or carbohydrate (HTCA) incorporation. The absence of adaptation to a specific light field is likely to benefit these populations because the mixed layer encompasses the entire euphotic zone (mixed layer ~10 m, 1% I_0 ~11.5 m).

Time Course and Diel Components of Photosynthesis

While absolute uptake and biochemical assimilation of $^{14}CO_2$ and $^{35}SO_4^{2-}$ are influenced by light intensity, both duration of light incubation and time of day also may be important in the products of photosynthesis over the 24-h light/dark cycle. The interaction of these factors will be described using the light gradient experiment of 24 August at inshore station 401 (Fig. 4).

It is first necessary to emphasize the difference between ^{14}C distribution (as percent of total fixed carbon) and the amount of carbon fixed into specific components. In this example, although the proportion of ^{14}C in protein decreases with increasing irradiance (Fig. 4B), the amount of ^{14}C in protein increases and the effect of photoinhibition is less severe than for other fractions (Fig. 4C). Furthermore, incorporation of ^{14}C into protein was light saturated at lower irradiance than total ^{14}C uptake. Consideration of both proportional and absolute subcellular isotope distribution is thus essential for interpretation of isotope incorporation data.

Total carbon dioxide fixation was light saturated between 336 and 760 μEinst.·m^{-2}·s^{-1} and displayed a photoinhibitory response at 1680 μEinst.·m^{-2}·s^{-1} (Fig. 4A). The extent of photoinhibition was the same for all incubation times, averaging 57% reduction of photosynthesis relative to P_{opt} (336 μEinst.·m^{-2}·s^{-1}). Dark carbon dioxide uptake was less than 2% of the light-saturated rate for all time points.

Light intensity strongly influenced the subcellular distribution of newly fixed carbon, represented in Fig. 4B for the full-day (14.8 h) incubation. The most pronounced effect was on the proportion of carbon incorporated into protein. Dark metabolism resulted in over 50% of the total ^{14}C appearing in the protein fraction whereas only 15% was found in protein at the optimum light intensities. At photoinhibiting light intensity (1680 μEinst.·m^{-2}·s^{-1}) there was also an increase in percent carbon incorporation into protein, while total carbon fixation was decreased by 57% relative to P_{opt}. Conversely, assimilation of carbon into lipids was directly proportional to light intensity and showed no indication of photoinhibition (as percent of total fixed carbon). Both LMW and HTCA-soluble (nucleic acid and carbohydrate) carbon increased from dark incorporation levels to a small extent (not shown) reaching a relatively stable plateau near the lower bound of saturating light intensities; however, by far the most significant effects of light intensity were on protein and lipid incorporation.

In all cases during this study, photoinhibition was accompanied by an increase in the percentage of $^{14}CO_2$-C in protein, indicating that protein synthesis was less adversely affected by high light than other biosynthetic reactions. The proportion of

TABLE 2. Effect of incubation time on P_{opt}:dark uptake ratios for $^{35}SO_4$-S and $^{14}CO_2$-C at station 401 on 24 August 1982. P_{opt} data are from the 336 μEinst.·m^{-2}·s^{-1} light level.

Hours of incubation	Carbon (μg·L^{-1})			Sulfur (ng·L^{-1})		
	P_{opt}	Dark	P_{opt}:dark	P_{opt}	Dark	P_{opt}:dark
3.9	30.62	0.53	57.8	270.6[a]	136.7	2.0
8.0	59.38	0.74	80.2	510.9	199.2	2.6
14.8	92.57	1.14	81.2	757.2	215.2	3.5

[a] P_{opt} value from 756 μEinst.·m^{-2}·s^{-1} light level due to loss.

carbon in protein was lowest at optimum light intensities for photosynthesis.

Sulfate uptake was also a positive function of light intensity (Fig. 5A) and incubation time, but there were several important differences between carbon and sulfur uptake. There was a much smaller photoinhibitory response at the highest light intensity, but inhibition increased with incubation time from 14% at 3.9 h to 28% for the full-day (14.8 h) incubation. It was also immediately apparent that the ratio of light-saturated to dark sulfate uptake was much lower than for $^{14}CO_2$ fixation, particularly in the short incubation. Light enhancement of sulfate uptake (P_{opt}:dark) increased with exposure time (Table 2) to a greater extent than for carbon fixation but reached only 5% of the maximum P_{opt}:dark ratio for carbon dioxide.

Light intensity exerted a smaller influence on the subcellular distribution of newly incorporated sulfur (Fig. 5B). A minor but very reproducible reduction in the percentage of sulfur in protein occurred with increasing light intensity. No influence whatsoever was seen in the proportion of either sulfur-containing lipids or LMW components, and the HTCA-soluble sulfur (primarily the ester-SO_4^- component) increased only at the highest light intensity. Note the much lower percent ester-SO_4^- relative to the early-season experiment (Fig. 2).

Other than the weak but consistent influence of exposure time on the P_{opt}:dark sulfate uptake ratio, there was no difference in the subcellular distribution of either $^{14}CO_2C$ or $^{35}SO_4$-S as a function of incubation time (Table 3). The consistent absence of incubation time effects in this study facilitates comparison of data from experiments of differing incubation time, as long as these are confined to the natural light period.

Night Metabolism

Carbon metabolism of algae at night, in the absence of net carbon dioxide fixation, became apparent only when the subcellular distribution of previously fixed carbon was examined during the night relative to that of samples harvested at the end of the light period. Due to the nature and extent of the redistribution of ^{14}C in the subcellular fractions (Fig. 6) and the low dark carbon dioxide fixation during day and night incubations, the contribution of incidental carbon dioxide fixation by chemolithotrophs and other nonphotosynthetic carbon dioxide fixing microorganisms was discounted. The events shown for the sample previously exposed to optimum photosynthetic light intensity (336 μEinst.·m^{-2}·s^{-1}) conformed to certain generalities regarding night algal metabolism: (1) protein-^{14}C continued to increase during the dark period at a rate not substantially different from the light-driven rate; (2) both HTCA (i.e. carbohydrate-containing) and LMW components lost ^{14}C; (3) lipid-^{14}C remained constant or increased slightly but did not

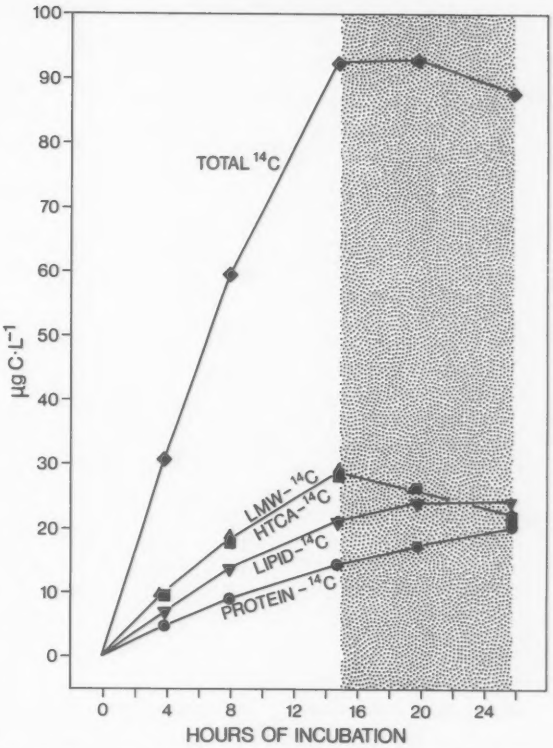

FIG. 6. Time course (24 h) of $^{14}CO_2$-C incorporation into macromolecular products at P_{opt} (336 μEinst.·m^{-2}·s^{-1}).

decrease at night; and (4) loss of total cellular ^{14}C occurred, but to a lesser extent than the sum of losses from LMW and HTCA compartments. The increase in protein-^{14}C therefore contained label derived from the LMW metabolic intermediates and/or carbohydrate reserves, both of which function as dual carbon and energy sources for night metabolism.

With respect to whole-cell elemental composition, night metabolism produced a relatively uniform effect at all but the lowest intensities of prior light exposure (Fig. 7). Small losses of ^{14}C, about 15% of that fixed during the day, were accompanied by much larger increases in total cellular ^{35}S, so the whole-cell ratio of ^{14}C:^{35}S dropped by almost 50% overnight (Fig. 7C).

As shown in Fig. 6, carbon from LMW intermediates and storage products was partially redistributed into the protein fraction at P_{opt} during night growth. This phenomenon was not restricted to samples previously exposed to optimum light. Total protein-^{14}C (Fig. 8A) and protein-^{35}S (Fig. 8B) both increased at night across the light gradient, and the overnight protein component retained the general shape of the day's P versus I curve. As in light-driven photosynthesis and protein synthesis, the photoinhibitory effect of the highest light intensity was more pronounced for ^{14}C incorporation into protein than for ^{35}S. In contrast with whole-cell results described above, however, there was little change in the protein ^{14}C:^{35}S ratio after overnight incubation (Fig. 8C). The ^{14}C:^{35}S ratio of the isolated protein for all light intensities compared favorably with the value of 48 derived from sequenced proteins (cf. Jukes et al.

TABLE 3. Percent distribution of $^{14}CO_2$-C and $^{35}SO_4$-S as a function of incubation time at station 401 on 24 August 1982. Data are given for two light levels: 140 and 336 μEinst.·m^{-2}·s^{-1}.

	Fraction % of total radioactivity											
	Carbon						Sulfur					
	Lipid		HTCA		Protein		LMW organic-S		Ester sulfate		Protein	
Hours of incubation	140	336	140	336	140	336	140	336	140	336	140	336
3.9	22.8	22.5	26.1	30.5	19.2	15.2	17.0	Lost	28.7	Lost	31.3	Lost
8.0	21.8	23.1	28.2	30.3	18.2	15.1	17.7	17.4	27.5	28.6	30.5	28.0
14.8	20.7	22.8	25.8	30.2	17.3	15.4	17.2	19.2	25.1	24.8	31.8	30.2

1975), suggesting that carbon dioxide fixing microorganisms dominated the assimilation of sulfate into protein and that heterotrophic microorganisms accounted for a relatively small proportion of total net protein synthesis in the upper water column. Figure 8D shows the night-only increase in protein-^{14}C and protein-^{35}S, which further emphasizes the prior light dependence of night protein synthesis. The proportion of protein synthesized at night, based on the ^{35}S data, was about 50% of the light day amount or 30% of the full 24-h production, in balance with the proportion of light in the 15 L:9 D cycle. Thus, rates of night protein synthesis were nearly equal to daytime rates.

It is necessary to differentiate between incubation time dependence and time-of-day dependence when considering temporal changes of biochemical composition measured by radioisotopic methods. Fortunately, in the great majority of cases in this study, assimilation of ^{14}C-labeled bicarbonate during light incubation proceeded with uniform incorporation of carbon into the major end products of photosynthesis. For the experiment of 24 August, the relative subcellular distribution of both ^{14}C and ^{35}S was constant throughout the light day (Fig. 9). The redistribution of ^{14}C at night was readily discernible as increased percent ^{14}C in protein and to a lesser extent in lipid as protein synthesis utilized carbon from LMW and carbohydrate compartments. Combined with a small overall loss of ^{14}C due to respiratory energy production, the proportional distribution reflected the net flows depicted in Fig. 6. Sulfur requirements for net protein synthesis at night were met with exogenous $^{35}SO_4^{2-}$, and there was no change in subcellular distribution of ^{35}S at any time.

Night protein synthesis and carbohydrate degradation were dependent on prior light exposure. Ratios of the nutritionally significant carbon-containing biopolymers to one another were also sensitive to prior light history (Fig. 10) and graphically illustrated the potential alteration of cellular composition by night metabolism. In the dark, protein was the major sink for carbon, with little incorporatin of ^{14}C-labeled bicarbonate into lipid. The absence of a light/dark cycle prevented change of the resultingly high ratios of protein to other polymers. Subsaturating light (55 μEinst.·m^{-2}·s^{-1}) produced overnight changes amplifying the dominance of protein in cellular composition. Prior light intensities promoting near-maximum but not photoinhibited carbon dioxide fixation (140-756 μEinst.·m^{-2}·s^{-1}) led to consistent night increases in protein:carbohydrate and protein:lipid, and dawn samples contained nearly equal proportions of ^{14}C in the three macromolecular components (Fig. 10). At photoinhibiting irradiances, the less pronounced inhibition of protein synthesis was reflected in higher ratios of protein to other components after overnight incubation.

Seasonal Effects: Temperature and Daylength

Prior to water column stratification the photosynthetic characteristics of surface and deepwater phytoplankton at the central Lake Ontario station 403 were very similar. On 11 June 1982, water from 1 and 150 m (water column depth 178 m) yielded similar total uptake of $^{14}CO_2$-C or $^{35}SO_4$-S in all-day incubations (Fig. 11). The percent ^{14}C incorporated into protein declined from a dark maximum of 25–35% to 4–6% at light saturation. The lowest light level, 8 μEinst.·m^{-2}·s^{-1}, was well resolved from the dark control, and light saturation was reached at lower light intensity than for inshore, stratified populations. There was no light intensity influence on the percent ^{35}S in protein, but a small increase did occur at all light intensities relative to the dark control. Ester-SO_4^- contained about 20% of the total assimilated sulfur.

During the season a total of 14 light intensity experiments were performed at the two major stations, encompassing a wide range of physical, chemical, and biological conditions. Comparison of potential photosynthesis and biochemical composition at P_{opt} with light intensity dependent trends in the pathways of $^{14}CO_2$ and $^{35}SO_4^{2-}$ assimilation (summarized in Table 4) permitted several generalities to be drawn from the study.

Sulfate uptake and incorporation of both carbon and sulfur into protein attained maximum light-stimulated rates at lower light intensities than total $^{14}CO_2$ fixation: the remaining photosynthetic potential was channeled largely into polymeric carbohydrate production and enhanced LMW metabolite pools. Consequently the proportion of ^{14}C incorporated into protein was always inversely related to light intensity. Relative synthesis of lipids generally increased with light intensity, but instances of no light effect were found, particularly during the short days of spring and fall. The relative incorporation of carbon into polysaccharides plus nucleic acids (HTCA) was surprisingly often inversely proportional to light intensity. Only weak trends, if any, were observed for protein-^{35}S as a percentage of the total label taken up.

We were most intrigued by seasonal trends of $^{14}CO_2$-C assimilation into macromolecular end products at P_{opt}. Among the many physical and nutritional influences experienced by the plankton during the April–November sampling period, water temperature and daylength emerged as the most important environmental factors controlling plankton metabolism and biochemical composition. While warming of surface waters

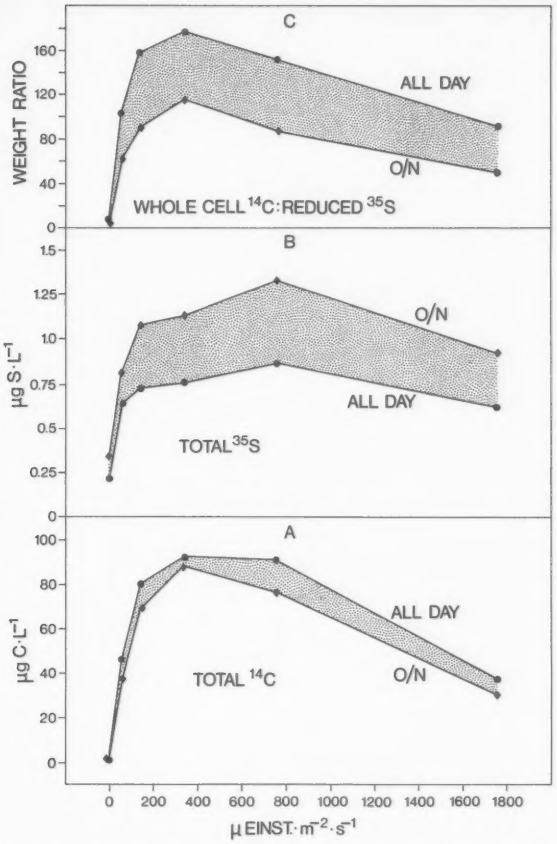

FIG. 7. Whole-cell uptake of (A) $^{14}CO_2$-C and (B) $^{35}SO_4$-S and (C) the whole-cell-^{14}C:reduced-^{35}S ratio (wt. wt.) as a function of light intensity for station 401 on 24 August. All day and overnight incubations are shown, with the net gain (Fig. 7B) or loss (Fig. 7A, 7C) of radioactivity shaded.

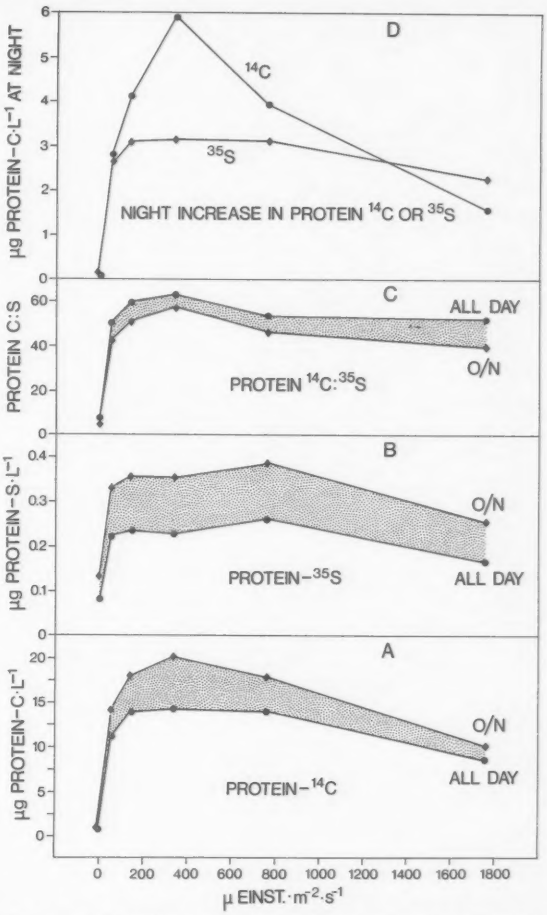

FIG. 8. Protein synthesis as a function of light intensity for station 401 on 24 August. All day and overnight incorporation of (A) $^{14}CO_2$-C and (B) $^{35}SO_4$-S into residue protein, with (C) protein ^{14}C:^{35}S weight ratio and night only increase in protein ^{14}C and ^{35}S. Net gain (Fig. 8A, 8B) or loss (Fig. 8C) is shaded.

resulted in only mildly increased assimilation number at P_{opt} ($Q_{10} = 1.1$, $r^2 = 0.529$; not shown), incorporation of ^{14}C into protein was tightly coupled to temperature ($r^2 = 0.812$; Fig. 12D).

Carbohydrate synthesis (i.e. $^{14}CO_2$-C incorporation into the HTCA fraction) provides reserve energy for night metabolism and therefore may be expected to vary as a direct function of nightlength (Hitchcock 1980). At P_{opt} (data from Table 4), Lake Ontario phytoplankton accurately tracked the changing daylength with storage of energy reserve polymers (Fig. 12A): the longest day (i.e. shortest night), 21 June, is the vertex of a parabola describing the percentage of newly fixed $^{14}CO_2$-C incorporated into the HTCA-soluble fraction. The proportion of HTCA-^{14}C was quantitatively related to daylength ($r^2 = -0.933$), as demonstrated in Fig. 13.

The independent nature of temperature and daylength regulation of phytoplankton metabolism is demonstrated in part by the absence of correlation between percent carbon in HTCA and temperature (Fig. 12B) and the weak relationship between daylength and percent carbon in protein (Fig. 12C). The validity of daylength as a forcing function for carbohydrate storage is strengthened by experiments performed early in the season (paired sets including Julian days (138, 140), (160, 162), and (181, 183)). The very late development of thermal stratification at the central lake station fortuitously afforded an opportunity to compare carbon incorporation patterns of inshore, warmwater populations with plankton from cold water under identical day/night cycles. In the absence of daylength differences, phytoplankton at both stations produced identical proportions of HTCA material but had substantially different proportions of protein-C, with the offshore station yielding the lower percentage of protein-C. Therefore, physical factors such as temperature and daylength may, in some cases, prevent changes in cellular composition in response to other regulators such as nutrient deficiency (Myklestad and Haug 1972).

It is noteworthy that no temperature influence was recorded for the proportion of ^{35}S incorporated into protein. In fact, the percent sulfur in protein was relatively constant throughout the summer (Table 4), but during the spring, incorporation of ^{35}S-labeled sulfate into the ester-SO_4^- fraction was very high

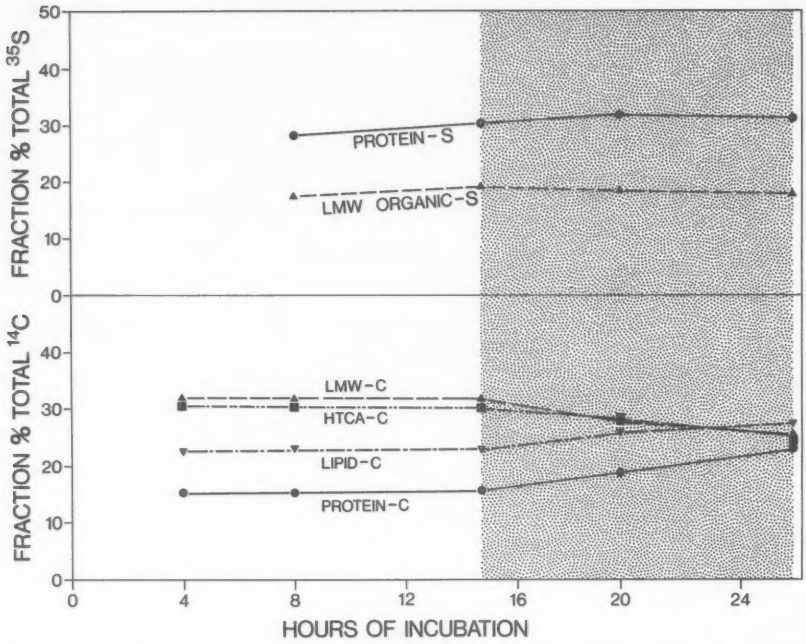

FIG. 9. Proportional distribution of $^{14}CO_2$-C (lower panel) and $^{35}SO_4$-S (upper panel) in LMW metabolites and macromolecular products during incubation at 336 μEinst.·m^{-2}·s^{-1}.

(>50% of the total sulfur assimilated). From June on the importance of this fraction declined steadily to minimum values (~15% of the total sulfur assimilated) in late August. No late-season increase was observed.

Discussion

The extent to which light stimulated ^{14}C-labeled bicarbonate uptake and controlled the metabolic fate of newly fixed carbon contrasted sharply with its mild enhancement of $^{35}SO_4^{2-}$ uptake and virtual impotence over the pathways of sulfate assimilation. The differences highlighted the manner in which photosynthetic microorganisms have adapted to maintain temporal continuity of growth in the energetically discontinuous environment imposed by the day/night cycle. Central metabolic processes imperative to growth (e.g. protein synthesis, nucleic acid synthesis, and repair) were uncoupled from the external source of energy and activated through an intermediate and continuously available internal supply. Reduced carbon acted as a storehouse of potential energy (as reducing power) as well as a precursor in biosynthesis. In addition to the primary value of making the night available for biosynthetic purposes, substantial shorter-term benefits were obtained: the biochemically facile dehydration/polymerization and hydrolytic mobilization of carbohydrate polymers involved monomers which were direct metabolites of the primary photosynthate and immediate precursors to the TCA cycle of structural transformation and rapid energy generation. Consequently, excess production of photosynthate could be rapidly channelled into storage material and just as readily recovered to supplement or replace insufficient photosynthetic production. The energetic buffering capacity and quick response potential of polymeric carbohydrate reserves could thus ameliorate the unpredictable, short-term disturbances caused by shading or mixing through the water column as well as power the anticipated biosynthetic activities of impending night.

Photosynthesis by definition is obligately dependent on light, and it is the products of carbon dioxide fixation that yield information on the relative physiological status of the phytoplankton. The occurrence of carbon in nearly all cellular constituents provided an opportunity for detailed observation of metabolic activities using $^{14}CO_2$, but it was correspondingly more difficult to interpret $^{14}CO_2$ incorporation data quantitatively, particularly at night. Because the process of protein synthesis itself was not directly light dependent, $^{35}SO_4^{2-}$ assimilation measurements reflected growth which integrated the recent light history of the population. Reduced sulfur was much more restricted in subcellular processes, and by virtue of its ready availability (as sulfate), luxury uptake or mass storage mechanisms have not been necessary. Uptake and reduction occurred as needed for biosynthesis and provided a direct, quantitative means for measuring protein synthesis. $^{14}CO_2$ enabled sensitive analysis of de novo photosynthetic production as a function of imposed variables and with respect to diverse metabolic pathways. The understanding gained from assimilation patterns of $^{14}CO_2$ was enhanced substantially through concurrent study of $^{35}SO_4^{2-}$ incorporation, which distinguished between net production and turnover (both of which incorporate carbon dioxide into biopolymers in the light) and was an effective tracer of night production in quantitative terms.

In the majority of our experiments, by far the greatest light intensity induced changes of carbon distribution occurred in the protein and lipid fractions. Frequently, no discernible effect was found in either carbohydrate plus nucleic acids (HTCA) or LMW components (Table 4). Similar experiments with pure

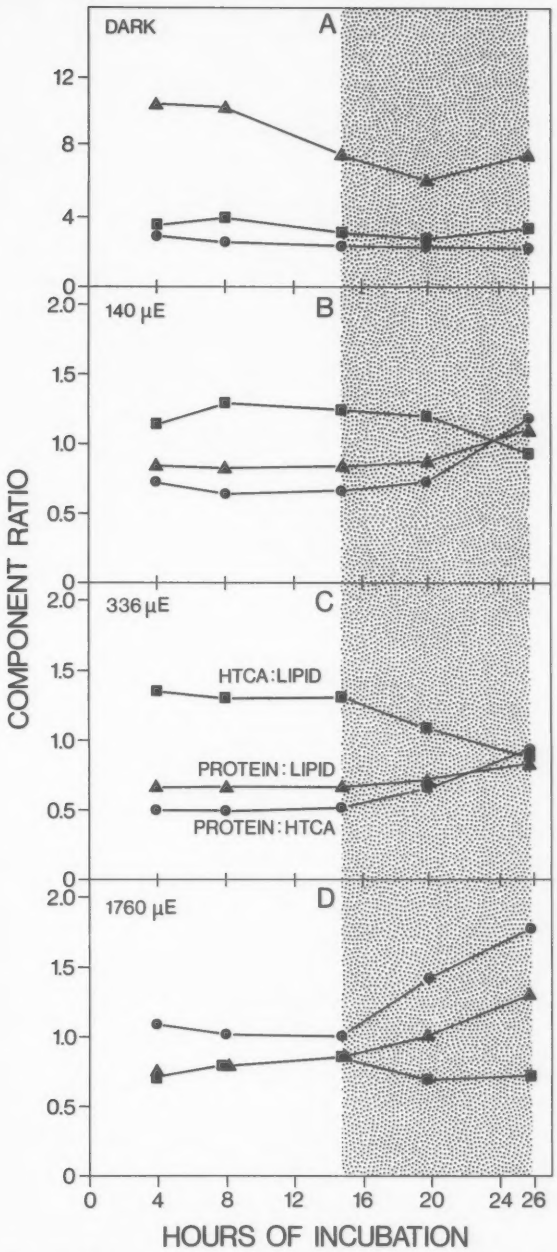

FIG. 10. Ratios of ^{14}C in newly synthesized major biopolymers throughout a day/night cycle as influenced by daytime light intensity exposure. Note scale change for dark control (Fig. 10A).

cultures and natural populations of Cyanobacteria (Konopka and Schnur 1980; Konopka and Schnur 1981) displayed much greater changes in HTCA-soluble and LMW components. These differences may be useful in identifying principal contributors to total photosynthesis in mixed populations, but better understanding of phylogenetic characteristics of macromolecular synthesis is required.

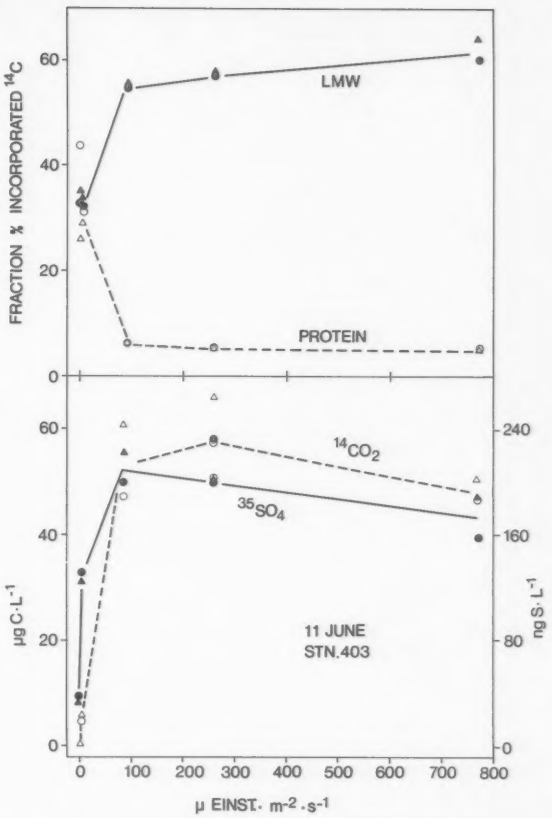

FIG. 11. Comparison of photosynthetic character between surface (1 m) and bottom water (150 m; water column depth 178 m) of Lake Ontario on 11 June, prior to seasonal stratification. Both panels: circles, 1-m samples; triangles, 150-m samples. Lower panel: total uptake of $^{14}CO_2$ (open symbols, broken line) and $^{35}SO_4$-S (closed symbols, solid line). Upper panel: proportional incorporation of $^{14}CO_2$-C into protein (open symbols, broken line) and LMW metabolites (closed symbols, solid line). All data are plotted.

For open-lake phytoplankton, the percentage of ^{14}C-labeled bicarbonate incorporated into protein in white light decreased with increasing light intensity, reaching a minimum at light saturation. This intensity-dependent relationship was also valid for red, blue, and green light exposure. During in situ incubations the percent ^{14}C in protein increases with depth below a minimum which is usually coincident with the depth of maximum photosynthesis and chlorophyll-specific assimilation efficiency (Cuhel and Lean 1987). Deeper penetration of blue-green light combined with decreasing light intensity complicates interpretation of in situ macromolecular synthesis patterns when the phytoplankton display chromatic adaptation, but for mixed-layer phytoplankton, light quality effects on total photosynthesis and its macromolecular end products were negligible. Thus for Lake Ontario plankton the depth of minimum percent ^{14}C in protein may be used as a bioassay for P_{opt}, especially when community structure and/or biomass varies markedly with depth. In such cases, the depth of maximum productivity may not necessarily be the same as the depth of biomass-specific maximum photosynthesis.

TABLE 4. Seasonal summary of photosynthetic parameters during light intensity experiments for the Lake Ontario Nutrient Assessment Study, 1982. Data are for 5-m samples unless indicated otherwise. Light intensity dependent changes in subcellular distribution are described as follows: NC, no change; POS, positive; NEG, negative. Values in parentheses indicate weak trends. N/A, not available.

					Fraction % total label at P_{opt}				Change in fraction % total label with increasing light intensity				Weight ratio, Tot.C:prot.	
					Carbon			Sulfur,	Carbon			Sulfur,		
Date	Stn.	Temp. (°C)	Chl *a* ($\mu g \cdot L^{-1}$)	Assim. No.[a]	Lipid	HTCA	Protein	Protein	Lipid	HTCA	Protein	Protein	Red.-S	C:S
6 Apr.	401	1.2	1.6	0.4	12.3	38.6	3.9	18.0	NC	NC	NEG	NC	109	9.7
18 May	403	2.4	1.7	1.0	15.5	21.4	6.5	9.3	POS	NC	NEG	NC	263	35.9
20 May	401	8.9	4.1	1.4	35.9	22.1	12.1	9.5	POS	NC	NEG	NC	70	25.7
9 June	401	10.4	2.9	1.3	34.9	17.7	13.6	26.7	POS	NEG	NEG	(NEG)	133	38.3
11 June	403[b]	3.2	1.9	1.7	18.8	18.5	4.7	28.2	(NEG)	NEG	NEG	NC	447	65.9
30 June	401	10.0	5.1	2.4	39.5	19.4	10.9	27.6	POS	NEG	NEG	(NEG)	135	32.7
2 July	403[c]	3.8	3.8	1.0	22.8	19.0	6.6	27.5	POS	(NEG)	NEG	NC	474	83.3
13 July	403	15.7	6.7	1.3	31.2	22.3	20.0	28.9	POS	NEG	NEG	NC	82	32.7
12 Aug.	403	18.7	2.5	3.7	21.3	26.2	20.3	N/A	POS	NEG	(NEG)	N/A	N/A	N/A
24 Aug.	401	14.5	4.4	1.4	22.8	30.2	15.4	30.2	POS	NC	NEG	(NEG)	176	62.5
25 Aug.	403	15.0	2.7	2.6	19.6	34.8	11.6	34.9	POS	NC	NEG	(NEG)	220	52.3
23 Sept.	403	16.0	3.5	2.9	17.0	36.3	12.4	7.0	NC	NC	NEG	NEG	58	88.5
20 Oct.	403	12.3	5.7	1.7	18.6	44.3	11.2	19.8	NC	NC	NEG	(NEG)	493	189.0
22 Nov.	403[d]	6.1	1.1	1.5	21.1	36.6	6.7	N/A	NC	NC	(NEG)	N/A	N/A	N/A

[a]Assimilation No. in g C·g Chl $a^{-1} \cdot h^{-1}$.
[b]Sample from 1 m.
[c]Sample from 20 m due to developing stratification.
[d]Incubation light/dark cycle 15 h out of phase.

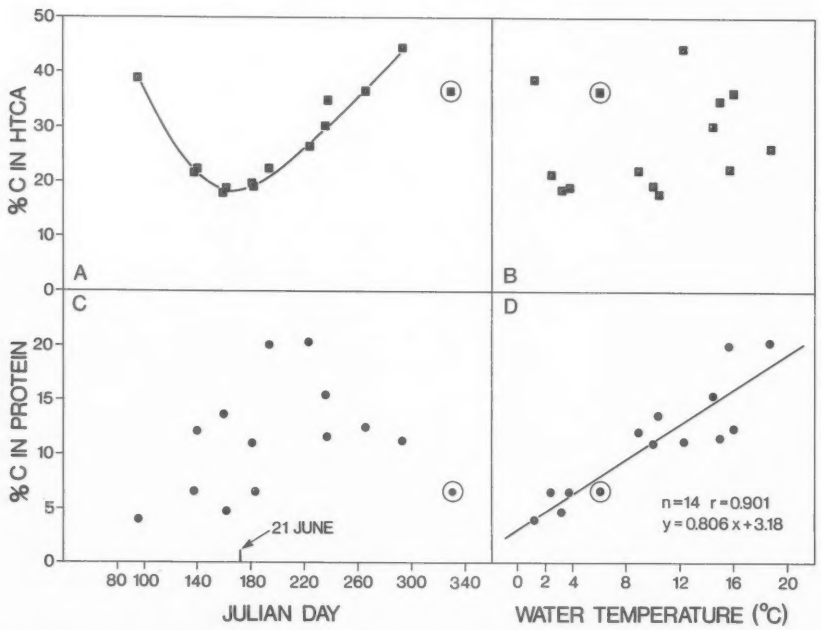

FIG. 12. Relative incorporation of $^{14}CO_2$-C into protein and carbohydrate-containing (HTCA) fractions of Lake Ontario phytoplankton as a function of water temperature and daylength (in chronological Julian days). (A and B) Incorporation into HTCA; (C and D) incorporation into protein. Water temperature at 5 m in Fig. 12B and 12D. Note: light/dark cycle was 15 h out of phase for the last experiment (JD 326; water temperature 6.1°C; data circled).

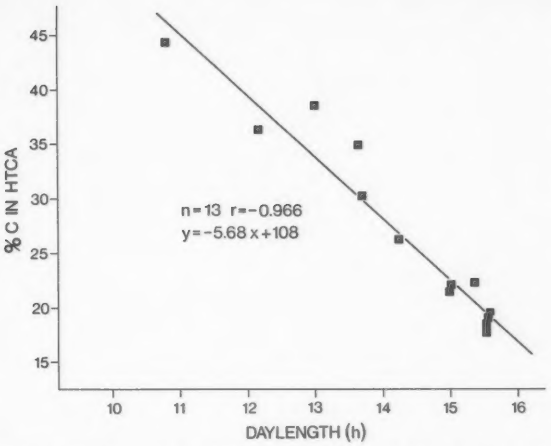

FIG. 13. Incorporation of $^{14}CO_2$-C into HTCA as a direct function of daylength for data from Fig. 12. The value from November (circled in Fig. 12) was excluded because of the improper light/dark cycle.

Light provided much less stimulation for sulfate uptake than for carbon dioxide, and the pathways of its assimilation were only weakly influenced by light intensity. Even though bacteria accounted for 50% of the biomass of lake plankton <20 μm in cross-section (Caron et al. 1985), a surprising number of indices such as the proportion of sulfur incorporated into protein (Roberts et al. 1963; Kelley et al. 1976), presence of sulfolipids (Benson 1963; Sinensky 1977), occurrence of carbohydrate polymer-bound inorganic sulfate (ester-SO_4^-; Ramus 1974; Percival et al. 1980), and parallel patterns of $^{14}CO_2$ and $^{35}SO_4^{2-}$ metabolism at night implicate photoautotrophs as the dominant producers of particulate protein in the surface microplankton community. Bacterial activity was however indicated by $^{35}SO_4^{2-}$ incorporation patterns in samples from the base of the euphotic zone/mixed layer in in situ incubations (Cuhel and Lean 1987).

We have found low P_{opt}:dark ratios for sulfate to be quite general for lake plankton throughout the year whereas marine plankton display more pronounced light enhancement of sulfate uptake (Cuhel et al. 1984). Low light:dark uptake ratios were also obtained by Monheimer (1981) at depths of >25% P_{max} in Lake St. George. Possible explanations include a large, light-independent component resulting from microheterotrophic activity or lack of direct coupling between incident light intensity and essential biosynthetic processes (e.g. protein and nucleic acid synthesis) in freshwater algae. As discussed above, we favor the latter for several reasons. In pure cultures of freshwater algae, Monheimer (1981) demonstrated that dark sulfate uptake often exceeded rates under low light, and the P_{opt}:dark ratios were low overall in short-term incubations. In both our light gradient and in situ studies, night rates of sulfate assimilation from optimal prior light exposures exceeded light rates from lower intensities or depths.

As an index of nutritional status of microplankton, the C:S ratio of whole cells is complementary to the C:N ratio. Like nitrogen, sulfur is primarily associated with essential growth factors (e.g. protein and nucleic acids) whereas carbon represents both growth-related and energy generation components. Lower C:S and C:N ratios imply more protein-rich composition and provide a gross indication of substantial change in plankton nutritional value resulting from night metabolism.

Continuation of protein synthesis at night, drawing on LMW and carbohydrate components of the plankton for both energy and amino acid skeletons, will result in increased protein:carbohydrate and protein:lipid ratios as predicted by the overnight decrease in whole-cell ^{14}C:^{35}S. The relative abundance of protein, carbohydrate, and lipid in microplankton has been shown to influence the growth rate and assimilation efficiency of herbivores (Scott 1980). Pure cultures of *Dunaliella tertiolecta* have been used to provide examples of the possible range of cellular composition (with respect to carbon, sulfur, nitrogen, protein, and carbohydrate) during phases of the day/night cycle (Cuhel et al. 1984). Night growth may be a factor resulting in diel cycles of microplankton nutritional value to herbivores. Our studies on Lake Ontario at first suggested that diel cycles in the biochemical composition of plankton occur and may be of significance to the trophodynamics of lake plankton.

Because of the higher proportion of protein-^{14}C at the beginning of the night for sub- and supersaturated light regimes, it was only during prior light exposures in the range of optimum photosynthesis that overnight metabolism produced plankton with uniform ratios of carbon-containing macromolecules, based on ^{14}C distribution. In all likelihood, protein carbon was even more abundant after night metabolism than suggested, due to the differing specific activity of carbon during night redistribution processes (see above).

The implications of Scott's (1980) work with a marine rotifer relate to the preferred food composition of a zooplankter obeying indeterminant growth. He found that the best growth and highest assimilation efficiencies were obtained when the food source contained an equal ration of protein (for biomass production), carbohydrate (for short-term energy generation), and lipid (for membrane synthesis and long-term maintenance energy during food inavailability). Based on the ^{14}C data presented above, zooplankton with these requirements would be best adapted to feeding in the middle euphotic zone late at night and near dawn, when night metabolism had altered the chemical composition of the food source to meet these criteria.

Other zooplankton may benefit from different food composition. For example, those with determinant growth will prefer a balanced food source during the growing stages (e.g. naupliar and copepodite stages) but may need more carbohydrate-rich food during mature stages when the energy-expensive process of reproduction is the dominant metabolic event. In addition, eggs contain a high proportion of energy reserves as either carbohydrate or lipid (cf. Taylor et al. 1987). Egg production by *Acartia clausi*, for example, was concentrated in the late night following major episodic feeding during the afternoon and early evening (Saint-Jean and Pagano 1983) when ingested energy reserves would be greatest. Thus, the varied chemical composition of algae at different depths in the water column and at different times in the day/night cycle may provide a useful range of foods from which zooplankton may select the optimum type required for their particular metabolic needs.

In addition to alterations of nutritional quality of plankton, night protein synthesis is a major component of energy metabolism resulting in net losses of fixed carbon from the plankton. Uptake of sulfate and its reductive assimilation into the sulfur-containing protein amino acids cysteine and methionine is an energy-expensive process on a molecular basis. Taking into account transport, activation, and reduction to the level of sulfide, incorporation of one molecule of sulfate into

protein requires approximately 21 ATP or high-energy equivalents. Since sulfur-containing amino acids account for about 3 mol % of total protein amino acids (Jukes et al. 1975), 33 peptide bonds (each requiring 5 ATP equivalents) are formed for each SO_4-S incorporated. Altogether the incorporation of 1 mol SO_4-S into protein requires about 190 mol of ATP, excluding biosynthetic requirements for generation of other amino acids and the carbon skeleton of the S-amino acids. Assuming that fixed carbon used for night respiration is reduced to the level of carbohydrate and allowing 38 mol of ATP generation for complete oxidation of each mole of glucose ($(CH_2O)_6$), we can estimate that 11 μg C must be oxidized for every 1 μg S (or 48 μg C) incorporated into protein. For the August 24 example described above (Fig. 6), night protein synthesis in the sample at P_{opt} incorporated 0.126 μg S, corresponding to oxidation of 1.4 μg CH_2O-C for energy. Total loss of ^{14}C at P_{opt} amounted to 4.5 μg C, i.e. 31% of the apparent night respiration can be accounted for by protein synthesis. The proportion of night ^{14}C respiration thus accounted for varied up to twofold within an experiment, but there was no systematic relationship to light intensity. Given that this calculation is the ratio of differences containing error, we have considered the average value for all nondark incubations within an experiment to be indicative of the energetic demands of night protein synthesis.

At this point it is necessary to reconsider terminology as it relates to ^{14}C versus CO_2-C. During daylight incubations of even slowly growing plankton populations, correction of ^{14}C-labeled bicarbonate uptake for ambient carbon dioxide concentration and isotope discrimination enables accurate measurement of total carbon fixation, since active increases in all LMW and macromolecular components occur. At night, however, this assumption may no longer be valid. There is little information available as to the compartmentalization of recently synthesized versus extant LMW and/or carbohydrate pools. We will assume that all carbohydrate polymers are equally available for degradation and metabolism at night. The carbon flowing from these compounds into either protein synthesis or respiration will have a lower specific activity than that of the ^{14}C-labeled bicarbonate added at the start of the experiment, by a factor of approximately $(^{14}CH_2O)_n/[(^{14}CH_2O)_n + (^{12}CH_2O)_n]$, where n indicates polymeric material and the ^{12}C term is the initial phytoplankton content of carbohydrate. If the daytime production of $(CH_2O)_n$ equals the cell contents at dawn, night processes may be underestimated by up to 50% due to isotopic dilution from carbohydrate catabolism. Night respiratory loss of ^{14}C from daylight incubations therefore can only be considered as a minimum unless greater than three doublings of phytoplankton biomass occur during the light period of isotope labeling (Taylor 1979).

In contrast, night metabolism and protein synthesis utilize exogenous sulfur (as sulfate) rather than internal pools (Cuhel et al. 1984). Thus, net increases in total and protein sulfur occur, with the same relative distribution of the newly fixed sulfate among metabolic products. In this case, the specific activity of the sulfur incorporated at night remains the same as that of the added tracer, and quantitative measurements are achieved. As a result, the incorporation ratios of ^{14}C:^{35}S will be less than the true weight ratio by the factor described above. In all cases, however, the amount of carbon flux will be underestimated by ^{14}C.

We now recognize that night protein synthesis is an important component in overall primary production. In most cases the proportion of protein synthesized at night was in accordance with the relative length of the night period, resulting in nearly continuous protein synthesis throughout the day/night cycle.

Night protein synthesis has implications for several aspects of lake dynamics. Obviously, the increase of protein to the food web is a primary consideration. Since few studies have been directed specifically towards estimation of protein production, no revision of current dogma is necessary. However, future studies in this area should take night growth into account. An indirect effect on nutrient cycling results from the need for plankton to assimilate nitrogen, as either nitrate or ammonium, from the water column to support amino acid synthesis. Accumulation of excess nitrate-N during the day or continuous utilization of NH_4^+-N may contribute significantly to total nitrogen dynamics.

When the mixed layer is deep and reaches below the depth of 1% I_0, as in many oceanic environments, circulation of cells throughout the mixed layer may prevent sufficient light exposure to enable night metabolism. Lake Ontario has a summer mixed layer of about 10 m, which corresponds to 1–5% of surface light intensity. However, the depth of maximum assimilation number for in situ incubated samples was usually 5 m at midday, above which apparent photoinhibition occurred (Cuhel and Lean 1987). The results of concurrent studies of DCMU-enhanced fluorescence in incubator, in situ, and freshly collected water samples demonstrated that the apparent photoinhibition found for static incubations was not realized by natural populations due to advective removal from high surface light intensities (Putt et al. 1987). The argument holds equally well for limited residence time in the very light-limited bottom of the mixed layer. It is likely that vertical profiles of night protein synthesis in situ would be uniformly high throughout the upper water column. Maintenance of subsurface maxima of night protein synthesis (Cuhel and Lean 1987) is probably as rare as the associated daytime primary productivity profile resulting from photoinhibition of samples held at fixed depth.

Prolonged exposure below the mixed layer (e.g. at 15 m depth) can also have a significant effect on biochemical composition. Although both production and night synthesis are low, due to light intensity effects on the immediate incorporation patterns of CO_2-C the net effect is production of relatively protein-rich food. This physiological stratification may also influence vertical distributions of zooplankton.

We have discussed the potential changes in biochemical composition of microplankton resulting from night increases in protein at the expense of carbohydrate reserves, based on changes in the subcellular distribution of newly incorporated $^{14}CO_2$-C during night metabolism. In order for the observed alterations to actually influence the entire standing crop of plankton, it is necessary that the growth rate of the microplankton be sufficiently fast that one night's metabolism can significantly increase protein relative to carbohydrate and/or lipid. For this condition to be met, population doubling times must be on the order of 1 d or less. In Lake Ontario, however, such growth rates are rarely encountered. Estimates of doubling times for total particulate organic carbon (POC) and protein, based on $^{14}CO_2$-C uptake and $^{14}CO_2$-C or ^{35}S-labeled sulfate assimilation into protein, are given in Table 5 for light intensity experiments and in Cuhel and Lean (1987) for in situ work. A significant discrepancy between POC and protein doubling times exists, although protein doubling times estimated from ^{14}C and ^{35}S incorporation into protein generally agree well. In any case, the growth rates are at best slow and not sufficient for

TABLE 5. Standing crops of POC and protein at 5 m, with 24-h production of POC and protein by $^{14}CO_2$-C and protein by $^{35}SO_4$-S assimilation techniques. All values are $\mu g \cdot L^{-1}$. Protein production based on CO_2-C or SO_4-S are presented as protein based on 52% C and 1% S in protein by weight.

		Standing crop		24-h production			Days to double		
				POC,	Protein		POC,	Protein	
Date	Stn.	POC	Protein	^{14}C	^{14}C	^{35}S	^{14}C	^{14}C	^{35}S
9 June	401	328	326	40.1	17.5	31.4	8.2	18.6	10.4
11 June	403	194	123	47.0	5.8	6.3	4.1	21.1	19.4
30 June	401	434	394	153.5	60.4	99.5	2.8	6.5	4.0
2 July[a]	403	516	218	50.0	8.1	6.9	10.3	26.9	31.6
24 Aug.	401	457	323	88.1	38.8	35.4	5.2	8.3	9.1
25 Aug.	403	314	353	80.7	34.0	33.1	3.9	10.4	10.7

[a]20-m sample.

night growth to effect changes in total plankton crop composition. Perhaps this contributes to the lack of significant vertical migration of zooplankton in Lake Ontario (Taylor et al. 1987).

Environmentally imposed physical factors appear to have a large influence on phytoplankton growth rate and biochemical composition. Water temperature places an upper limit on cell division frequency (Eppley 1972) and may exert equally strong regulation of cell composition. Relative incorporation of carbon into protein at optimum light was shown to be directly proportional to water temperature in Lake Ontario, consistent with pure culture (Morris and Farrel 1971) and field data from marine environments (Morris et al. 1981; Cuhel et al. 1984). Water temperature sets the maximum potential growth rate of phytoplankton (Eppley 1972), and it may influence the biochemical composition (and hence nutritional value) of the phytoplankton as well.

A second significant factor, daylength, was well correlated with relative production of carbohydrate, the principal energy reserve for dark (night) metabolism of algae. This relationship has been demonstrated in pure culture as well (Hitchcock 1980). Comparison of temperature and daylength effects on the two processes indicates that they act independently on phytoplankton metabolism. These long-term controls may define limits of cellular composition within which superimposed short-term variables such as nutrient availability must operate.

The direct relationship between nightlength and carbohydrate synthesis suggests a relatively sophisticated seasonal timing mechanism in phytoplankton. Time-course measurements demonstrated the independence of relative carbon incorporation into carbohydrate from incubation time during the day, yet carbohydrate production was well related to the duration of the impending night. Moreover, the amount of storage far exceeds that required for "basal metabolism," suggesting that significant growth-related processes have been anticipated.

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Nitrogen Transformations in Lake Ontario

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Lean, D. R. S., and R. Knowles. 1987. Nitrogen transformations in Lake Ontario. Can. J. Fish. Aquat. Sci. 44: 2133–2143.

Concentrations of ammonium plus nitrite in Lake Ontario were highly correlated with ammonium regeneration from zooplankton excretion ($r = 0.966$), inferring that elevated nitrite concentrations result from nitrification. Nitrapyrin-sensitive dark ^{14}C-labeled bicarbonate assays confirmed high rates of nitrification by chemoautotrophic bacteria. ^{15}N-labeled nitrate experiments showed that nitrate, not ammonium, was the principal form of N used for total microbial protein synthesis. Size fractionation experiments also suggested that small cells were responsible for most of the ammonium uptake, while large cells used mostly nitrate. Nitrate depletion in the surface waters during summer stratification resulted from movement to particulate N, nitrite, and ammonium as well as losses in particulate N due to sedimentation. At least one third, however, was unaccounted for (i.e. 30 mg $N \cdot m^{-2} \cdot d^{-1}$) and may have been converted to protein which would move up the food chain to larger organisms (e.g. fish) not sampled during conventional water chemistry. Nitrous oxide profiles showed that nitrate losses through denitrification are unlikely to occur. Consequently, unless nitrate loading to Lake Ontario is reduced, nitrate concentrations should be expected to continue to increase.

On a établi une forte corrélation entre l'ensemble des concentrations d'ammonium et de nitrite dans le lac Ontario et la regénération de l'ammonium à partir de l'excrétion du zooplancton ($r = 0,966$), en supposant que les concentrations élevées de nitrite découlent de la nitrification. Des essais à l'obscurité avec du bicarbonate marqué au C^{14} sensible à la nitrapyrine ont confirmé les taux élevés de nitrification par les bactéries chimiautotrophes. Des expériences avec du nitrate marqué au N^{15} ont montré que le nitrate, et non l'ammonium, était la principale forme de N utilisé pour la synthèse totale des protéines microbiennes. Des expériences par fractionnement ont également donné à penser que les petites cellules étaient responsables de la plus grande partie de l'absorption d'ammonium tandis que les grosses cellules utilisaient surtout le nitrate. L'appauvrissement en nitrate dans les eaux superficielles pendant la stratification estivale a été le résultat de la transformation en azote particulaire, en nitrite et en ammonium de même que de pertes sous forme d'azote particulaire dues à la sédimentation. Cependant, un tiers au moins n'a pas été expliqué (c.-à-d. 30 mg $\cdot m^{-2} \cdot j^{-1}$) et pourrait avoir été converti en protéine, ce qui ferait remonter la chaîne alimentaire aux organismes plus gros (p. ex. les poissons) non échantillonnés au cours d'une analyse chimique conventionnelle de l'eau. Les profils de protoxyde d'azote ont montré que les pertes de nitrate par la dénitrification ont peu de chances de se produire. Par conséquent, à moins que l'apport de nitrate dans le lac Ontario ne soit réduit, on doit s'attendre à ce que les concentrations de nitrate continuent à augmenter.

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Our understanding of the important processes which occur as nitrogen moves through lake ecosystems is based largely on extrapolations from soil research, incomplete N budgets, and a few kinetic measurements. Consequently, factors which influence the seasonal concentration patterns of the nitrogenous forms remain hypothetical.

Because of the intermediate oxidation level of nitrite, an emphasis on factors which influence the concentration of this form is essential. Nitrite maxima have been observed in many of the world's oceans (Olson 1981a), in Lake Michigan (Mortonson and Brooks 1980), and in Lake Ontario in 1966 and 1967 (Dobson 1984). Nitrite maxima in the ocean have been thought to result from either ammonium oxidation by chemoautotrophic nitrifying bacteria (Brandhorst 1959; Olson 1981a; Ward et al. 1982) or phytoplankton excretion during assimilation and reduction of nitrate (Vaccaro and Ryther 1960). In the euphotic zone, where nitrate levels are often low, nitrite uptake would usually outweigh its production (Olson 1981a). Here, photoinhibition of nitrification is also possible (Olson 1981b) and chemical photolysis of nitrite must be considered (Zafiriou and True 1979).

Based on mass balance calculations, significant nitrification can also occur in the aerobic hypolimnia of lakes (Christofi et al. 1981; Takahashi et al. 1982; Verdouw and Dekkers 1982; Hall and Jeffries 1984). Evidence for nitrification also comes from studies of oxygen depletion rates (Wezernak and Gannon 1967).

Knowles and Lean (1987) found winter nitrification to be the major factor causing oxygen depletion in Lake St. George, Ontario.

Despite the great sensitivity of ^{15}N stable isotope techniques, data on uptake of nitrate, nitrite, ammonium, and urea are not without problems of interpretation and rarely can be extrapolated to ambient concentrations (Glibert et al. 1982, 1985; Wheeler et al. 1982; Laws 1984). In Lake Ontario, due to the high ambient nitrate concentrations, uptake rates are always maximal, but the low concentrations of ammonium make kinetics for this form difficult to interpret (Murphy 1980; Lean et al. 1983).

Limnologists have often considered that the nitrate decline in May–June in many temperate lakes was due to algal assimilation (e.g. Burns 1976), but a corresponding increase in particulate N does not always occur. In the present investigation, the seasonal concentration patterns of nitrogenous forms were related to uptake rates of ammonium and nitrate, estimates for nitrification, N sedimentation, and ammonium regeneration from zooplankton excretion. In this way, the major N pathways in the Lake Ontario ecosystem could be identified.

Methods

Experiments were conducted in Lake Ontario in 1982 as part of the LONAS study along the transect extending from northshore station 401, near Cobourg, Ontario, to southshore station 405 with emphasis on transport rates measured at midlake station 403 (Lean 1987; Simons and Schertzer 1987). As in previous limnological surveys on Lake Ontario (Stadelmann and Fraser 1974; Dobson 1984), samples from discrete depths were filtered through 0.45-μm (Sartorius 11103) membrane filters, with concentrations of nitrite, nitrate, and ammonium usually determined immediately using a Technicon II autoanalyser. Values for total Kjeldahl N were obtained on filtered samples maintained at 4°C and analysed within 1 wk. Total particulate N was measured using a Hewlett-Packard CN analyser. All methods are described in Environment Canada (1979).

Dark incorporation of radioactive bicarbonate in the presence and absence of the inhibitor nitrapyrin has been used as an index of nitrification (Billen 1976; Somville 1978; Vincent and Downes 1981; Vincent et al. 1981; Hall 1982; Knowles and Lean 1987). In the following experiments, samples were obtained with 6-L Niskin bottles and transferred to 300-mL BOD bottles, keeping the tube at the bottom of the bottle and allowing water to overflow for 10–15 s to avoid changes in dissolved gas concentrations. Just prior to incubation, 20 μL of analytical grade nitrapyrin (2-chloro-6-(trichloromethyl)pyridine) from Dow Chemical, dissolved in dimethyl sulfoxide (DMSO), was added to each BOD bottle giving a final nitrapyrin concentration of 20 $mg \cdot L^{-1}$. ^{14}C-Labeled bicarbonate (Amersham) was added to a final concentration of about 10^6 $dpm \cdot mL^{-1}$.

Measurements of nitrous oxide were conducted as described by Knowles et al. (1981). Water samples were placed in 350-mL sealed bottles without a headspace along with 1 mL of saturated $HgCl_2$. Nitrous oxide was determined by multiple phase equilibrium and gas chromatography with ^{63}Ni electron capture detection.

Assimilation of ^{15}N-labeled nitrate and ^{15}N-labeled ammonium was determined using a Jasco emission spectrometer (NAJI-1) (Murphy 1980). Dried filters (preignited 25-mm Whatman GF/F) containing the collected particulate material were put into discharge tubes with CuO powder as a catalyst. The tubes were sealed after evacuation to 0.01 Pa, combusted at 590°C for 16 h, and allowed to cool for 24 h. Each sample required only 10 μg of N for good emission. Uptake velocity was calculated using the following formula:

$$v = \frac{\%\ \text{excess}\ ^{15}N\ \text{in seston} \times \text{particulate N}}{\%\ \text{excess}\ ^{15}N\ \text{in}\ NH_4\ \text{or}\ NO_3 \times \text{time}}.$$

^{15}N-labeled ammonium chloride and ^{15}N-labeled sodium nitrate were supplied as 97 ^{15}N atom % (Biorad). ^{14}C Uptake was measured as described in Lean et al. (1987). Samples were incubated in a temperature-controlled incubator with light levels from a quartz-halogen fluorescent street light controlled by neutral density filters.

Results and Discussion

Seasonal Pattern for Nitrogen Partitioning

Concentrations of nitrite were in excess of 5 $\mu g\ N \cdot L^{-1}$ throughout most of the water column during the stratified period from early July to September (Fig. 1). At other times, values were usually 2–3 $\mu g\ N \cdot L^{-1}$. Nitrite concentration at station 403 peaked in August at over 10 $\mu g\ N \cdot L^{-1}$ (maximum 19). Station 401 (Fig. 1) and 405 (not shown) followed a similar pattern, but concentrations were slightly elevated during thermal bar conditions. Upwelling in October caused values at 401 to decline more abruptly than at other stations. Peak nitrite concentrations at each station across the lake (Fig. 2) illustrate the influence of thermal stratification patterns across the lake. The 12 $\mu g\ N \cdot L^{-1}$ isopleth approximates the depth of the epilimnion. The mixing depth is greater at station 405 (Simons and Schertzer 1987).

Instead of being restricted to the metalimnion as in 1966 and 1967 (Dobson 1984), elevated nitrite concentrations extended to the surface in 1982. Unlike that in 1972 (Stadelmann and Fraser 1974) and before, nitrate concentrations remained above 130 $\mu g\ N \cdot L^{-1}$ (see below Fig. 4, and Stevens and Neilson 1987). As such, nitrite utilization may be reduced in the surface waters. In 1972, when nitrate levels were low ($<5\ \mu g\ N \cdot L^{-1}$), nitrite uptake would probably outweigh its production.

At station 403, ammonium values were 2–3 $\mu g\ N \cdot L^{-1}$ until the end of June (Fig. 3) when ammonium concentrations began to increase. By August, metalimnetic values exceeded 10 $\mu g\ N \cdot L^{-1}$. Through September and October, higher ammonium values extended into surface waters. Below 50 m, ammonium concentrations were usually less than 3 $\mu g\ N \cdot L^{-1}$ throughout the season except in September and October. By November, ammonium values returned to the 1–2 $\mu g\ N \cdot L^{-1}$ range.

At 401 (Fig. 3, upper panel), the elevated ammonium values appear earlier in the summer and, like those for nitrite (Fig. 1), declined sooner in the fall due to an October upwelling event. Station 405, which was similar to 401 at other times of the year, received warm surface waters causing high ammonium values in October at 30–36 $\mu g\ N \cdot L^{-1}$ (not shown).

Seasonal changes in the depth distribution of nitrogenous forms are illustrated by comparing values for 8–11 June with those for 20–23 September (Fig. 4). Thermal bar conditions existed in June (Simons and Schertzer 1987), with surface temperatures of 10–11°C down to 5 m at 401 and 405, while the midlake was isothermal at about 3°C. Nitrate was depleted in the surface waters at 403 from 360 to about 130 $\mu g\ N \cdot L^{-1}$. When this decrease was integrated over the top 40 m, 6215 $mg\ N \cdot m^{-2}$ was converted to other forms. The increase in particulate N,

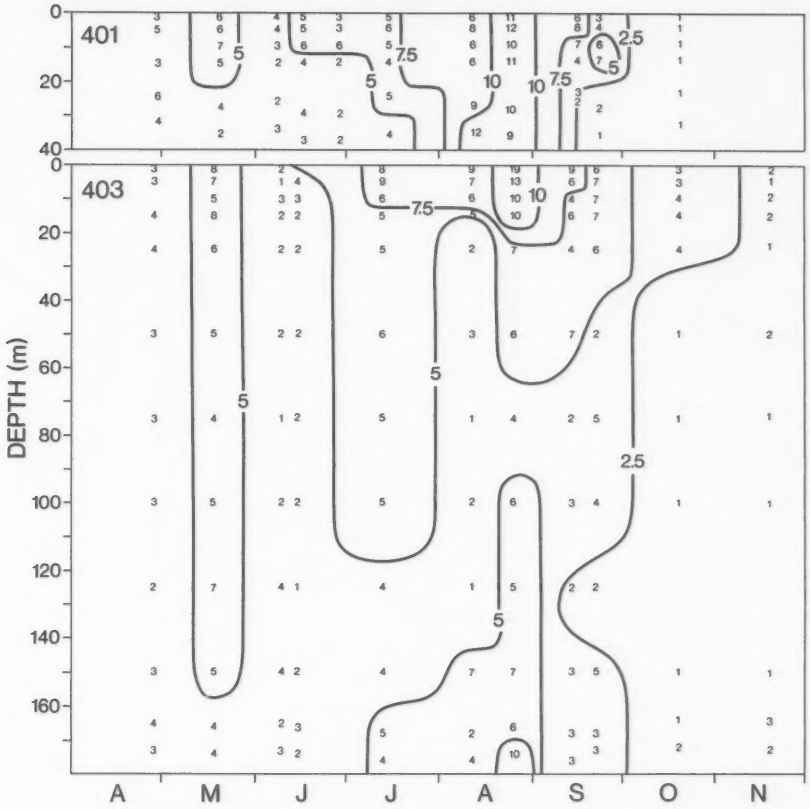

FIG. 1. Isopleths of nitrite concentration ($\mu g\ N \cdot L^{-1}$) from April to November 1982 at stations 401 (top) and 403 (bottom).

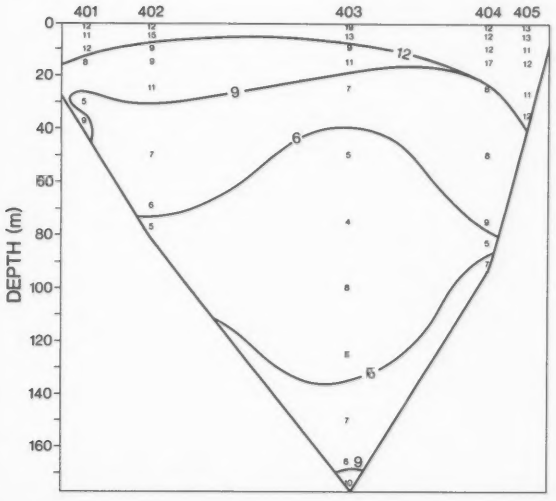

FIG. 2. Isopleths of nitrite concentration ($\mu g\ N \cdot L^{-1}$) across the lake at peak nitrite levels (24–27 August).

nitrite, and ammonium accounted for only 1250, 326, and 242 mg $N \cdot m^{-2}$, respectively.

Other protential losses of N were considered. N sedimentation, measured with sediment traps located at 40 m (Lean et al. 1987), was 1909 mg $N \cdot m^{-2}$ during this period. No significant changes in dissolved organic nitrogen were observed, with values in surface waters remaining near $210 \pm 16\ \mu g\ N \cdot L^{-1}$. Consequently, only 3727 of the 6215 mg $N \cdot m^{-2}$ can be accounted for. Input of N to surface waters was not measured, so the difference, which has yet to be explained, is a conservative estimate.

Denitrification must also be considered as a potential sink for nitrate-N. However, conditions in Lake Ontario leave little opportunity for denitrification even late in the season. For example, on 23 September at station 403 (Fig. 5) the temperature of the epilimnion was 16.1°C, with the metalimnion extending from 15 to about 50 m. Oxygen concentrations were near saturation except at 25 m (91% saturation) and within 10 m of the sediments (87%). For reasons that are not clear, nitrous oxide concentrations (Fig. 5) were below saturation and consistent with data from October and from Lemon and Lemon (1981) (Table 1). Consequently, Lake Ontario acts as a sink for atmospheric nitrous oxide (see Knowles et al. (1981) for discussion). This and the high oxygen concentrations suggest

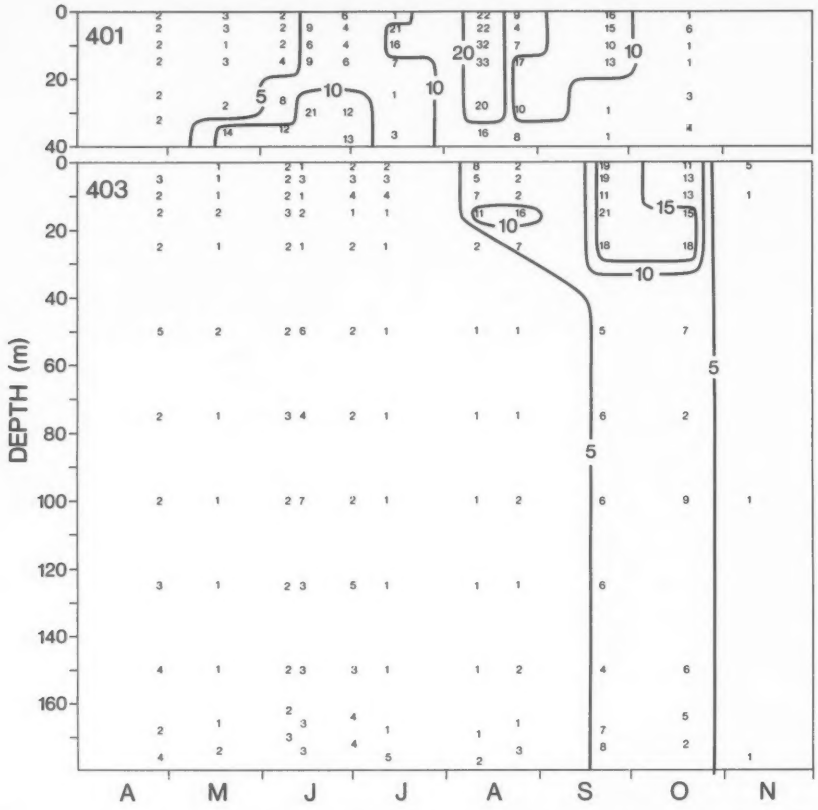

FIG. 3. Isopleths of ammonium concentration ($\mu g\ N \cdot L^{-1}$) from April to November 1982 at stations 401 (top) and 403 (bottom).

that denitrification in the water column is not a significant process for nitrate loss from Lake Ontario.

Below the euphotic zone (shaded area in Fig. 5), there was little accumulation of ammonium (Fig. 3, 4) resulting from decomposition, zooplankton excretion, and release of ammonium from sediment pore waters (Fig. 4). Ammonium concentrations were little changed from those in June, but nitrite and nitrate levels were higher near the sediments (Fig. 4). These observations are consistent with the hypothesis that in the deeper waters, regenerated ammonium is nitrified. Bioassays will be discussed below which support this view.

Cuhel and Lean (1987a, 1987b) provided estimates of protein production based on ^{14}C-labeled bicarbonate and ^{35}S-labeled sulfate assimilation. Values were converted to protein based on 52% C and 1% S. These results can now be converted to N assuming that the percent N in protein was 17 (Jukes et al. 1975). Prior to thermal stratification, protein synthesis was low as was nitrate depletion. During the summer period, protein synthesis averaged about 300 mg protein$\cdot m^{-2} \cdot d^{-1}$ (Cuhel and Lean 1987a). This quantity times the 85-d period of stratification to 22 September (times 0.17 to convert to protein N) gives a value of 4335 mg $N \cdot m^{-2}$. If half of this quantity were transferred to larger organisms not sampled, it would account for the N "lost" from our budget. In other words the community would have a N or protein assimilation efficiency of approximately 50%.

Zooplankton Excretion

The release of ammonium through zooplankton excretion depends on the *community* assimilation efficiency rather than the *individual* or trophic level assimilation efficiency. If the zooplankton population was not expanding, i.e. growth was equal to losses through mortality, only a fraction of the N assimilated by zooplankton would be moved up the food chain. At higher trophic levels the assimilation efficiency is lower. This illustrates the important role of fish in aquatic nutrient cycles. A community that is not expanding has an assimilation efficiency of zero.

The influence of microzooplankton (Taylor and Heynen 1987) and heterotrophic microflagellates (Pick and Caron 1987) was neglected. The filtering rate of small animals (30–64 μm) was small relative to the >64 μm animals (Lean et al. 1987). Heterotrophic microflagellates have been shown to be significant in ammonium regeneration in marine systems (Goldman et al. 1985), but their overall importance in nutrient regeneration

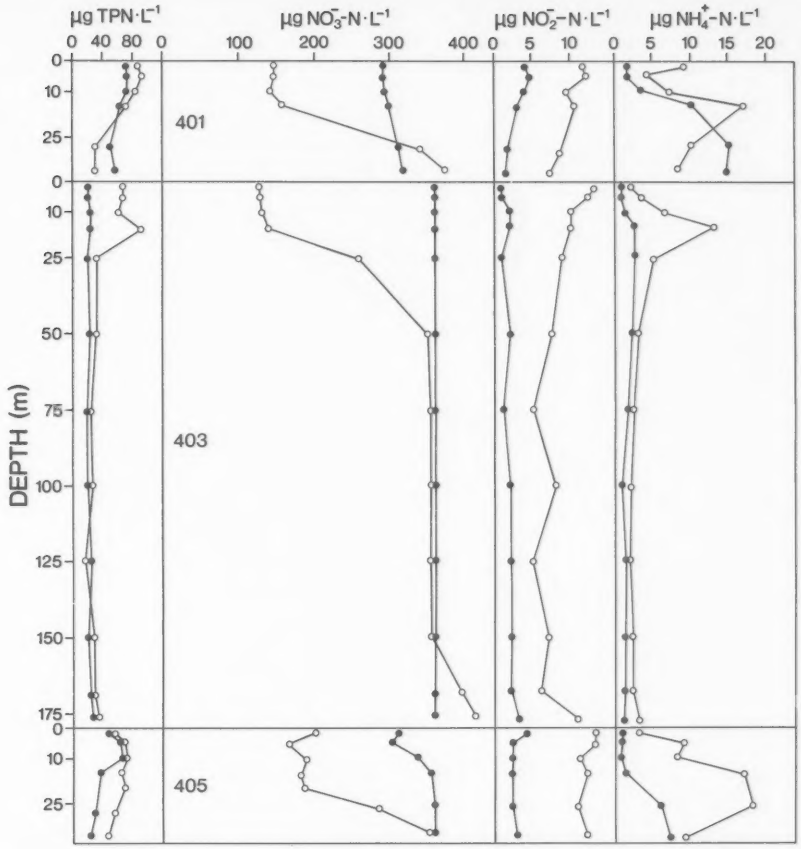

FIG. 4. Depth profiles of total particulate nitrogen (TPN), nitrate, nitrite, and ammonium concentrations measured on 8–11 June (solid symbols) and 21–23 September (open symbols) at stations 401 (top), 403 (middle), and 405 (bottom).

cannot be quantified at this time. Since they are food for macrozooplankton and if their net growth is zero, their N assimilated is included in the feeding rate calculation for the >64 µm animals. Consequently, for the following calculations it is recognized that the community assimilation efficiency is unknown but initially the calculation is made assuming it is zero.

Values for particulate N parallel those for chlorophyll *a* in the surface waters, increasing at 15 m and then continuing proportionately higher than chlorophyll throughout the water column (Fig. 5). Assuming that all particulate N was edible and assimilation efficiency was zero, the product of zooplankton grazing (from Lean et al. 1987) and particulate N provided an estimate for ammonium regeneration by major (>64 µm) zooplankton (Fig. 5, right-hand panel). During this period (21–23 September), regeneration rates would be about 0.2 µg $N \cdot L^{-1} \cdot d^{-1}$ in the deep water and 5.8 µg $N \cdot L^{-1} \cdot d^{-1}$ in the upper 20 m (Table 2).

Data obtained throughout 1982 were treated as above. Filtering rates were averaged over the epilimnetic zone over 24 h and multiplied by the mean particulate N (0–15 m). The product was plotted against ammonium concentrations (1–15 m). This relationship (Fig. 6) was significant ($r = 0.838$), but the sum of ammonium plus nitrite was even better correlated with regeneration (Fig. 6) ($r = 0.966$). If uptake rates of ammonium and nitrite were small, the observed concentration represents 4 d (slope of regression) of zooplankton excretion assuming an assimilation efficiency of zero. However, if assimilation efficiency was 50%, the quantity would represent 8 d of excretion and can account for the "lost" N from the seasonal N budget discussed above. These are minimum estimates, for the reassimilation is certainly not zero. Integrating these rates will be a challenge for future investigations.

Nitrification

Nitrification by chemoautotrophic bacteria was estimated by the nitrapyrin-sensitive dark ^{14}C-labeled bicarbonate incorporation. For example, samples from 1–20 m collected on 23 September at 403 were incubated at 16°C, while samples from the rest of the water column were incubated at 4°C. Duplicate bottles generally compared well (Fig. 7). Data for 1–20 m

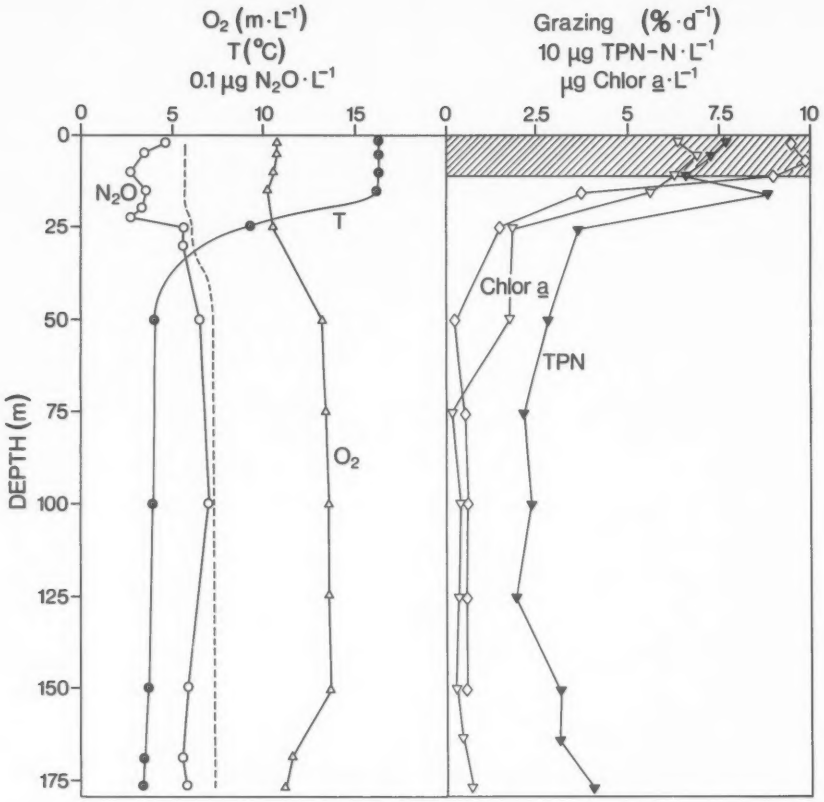

FIG. 5. Depth profiles of oxygen, temperature, and nitrous oxide (left). The broken line represents saturation levels for nitrous oxide. Concentrations of particulate nitrogen (×10), chlorophyll *a*, and zooplankton grazing (right). The euphotic zone (shaded area) extends from the surface to the depth of the 1% light level. Data from 21–23 September.

TABLE 1. Nitrous oxide concentrations (SD in parentheses) in 0–20 m and 25 m to bottom water depths.

	Nitrous oxide (µg·L^{-1})	
	0–20 m	25 m to bottom
21 September		
Station 405	0.42 (0.08)	0.50 (0.05)
Station 403	0.35 (0.07)	0.60 (0.05)
Station 401	0.39 (0.07)	0.55 (0.06)
20 October, station 403	0.31 (0.03)	0.46 (0.05)
September 1977 near station 405[a]	0.33	0.53

[a]From Lemon and Lemon (1981).

TABLE 2. Rates of N transformations at station 403 on 23 September 1982.

Depth (m)	Particulate N (µg·L^{-1})	Grazing (d^{-1})	Regeneration (µg N·L^{-1}·d^{-1})	Nitrification (µg N·L^{-1}·d^{-1})
0–20	75	0.0775	5.81	3.16
20–50	32	0.01	0.32	1.75
50–176	30	0.005	0.15	1.0

samples averaged 0.31 (±0.11), 25–50 m was 0.18, and 100–176 m was approximately 0.1 µg C·L^{-1}·d^{-1}. Converting C to micrograms of N oxidized, by dividing by 0.102 (Christofi et al. 1981), gives 3.16, 1.75, and 1.0 µg N·L^{-1}·d^{-1} for the three depth categories (Table 2). Although assimilation of ammonium by phytoplankton would be expected in the trophogenic zone, nitrification can account for over half of the ammonium released by zooplankton grazing in surface waters. In the deep waters, the nitrification assay suggests that these organisms have the potential to nitrify even more ammonium than is regenerated by major zooplankton excretion.

Additional data were obtained on October 20. Zooplankton grazing in the 0–20 m zone was 8%·d^{-1}, giving a regeneration rate of 3.3 µg N·L^{-1}·d^{-1}. Nitrification rates at ambient temperatures (12°C) provided values of 0.4–1.7 µg N·L^{-1}·d^{-1} for the 0–50 m zone. At this time of year, it appears that the nitrification rate was less than the regeneration rate. This may help to explain the observed increase in ammonium (Fig. 3).

Oxygen consumption associated with the oxidation of ammonium and nitrite to nitrate is 4.33 µg O_2·mg N^{-1} (Wezernak and Gannon 1967). Consequently, nitrification rates which aver-

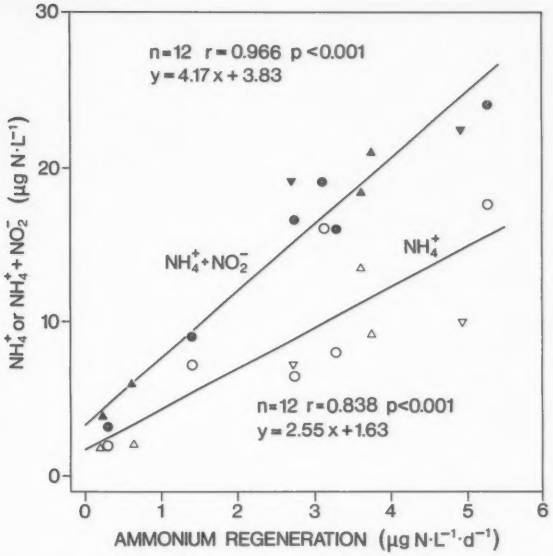

FIG. 6. Discrete depths 1–15 m averaged for ammonium alone (open symbols) and ammonium plus nitrite (solid symbols) as a function of ammonium regeneration (1–15 m average) at stations 401 (▲), 403 (●), and 405 (▼).

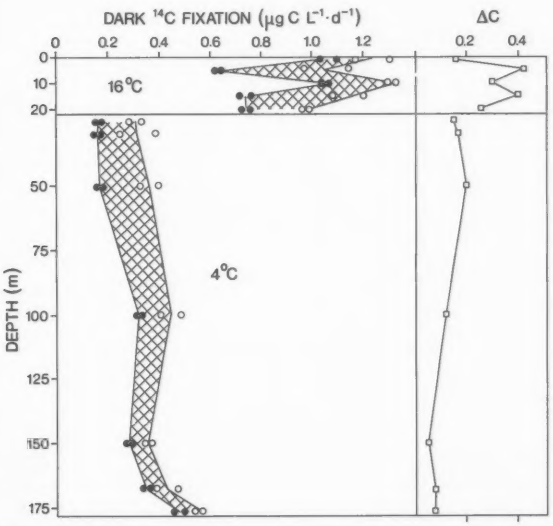

FIG. 7. Dark ^{14}C-labeled bicarbonate fixation for 0–20 m samples incubated at 16°C and 25–176 m samples incubated at 4°C with (●) and without (○) nitrapyrin. The difference (shaded area) is plotted as ΔC on the right. Data from 23 September.

aged 3.1 (±0.11) µg N·L^{-1}·d^{-1} require 0.6 µg O_2·L^{-1}·h^{-1}. Although further investigation is necessary, nitrification represents a significant component of total community respiration.

Ward et al. (1982) reported that nitrapyrin-sensitive chemoautrotrophic dark ^{14}C assimilation in a mixed population would be negligible. In our example, it was only 30% of the dark ^{14}C-labeled bicarbonate uptake in the surface waters but over 50% in the deeper samples (Fig. 7). Filter fractionation of

TABLE 3. Size distribution of dark ^{14}C-labeled bicarbonate uptake (3- to 6-h incubations).

Date	Station	Distribution (%) 0.2–1.0 m	1.0–5.0 m	>5.0 m
9 June	401	72	18	9
10 June	403	67	26	7
30 June	405	68	20	12

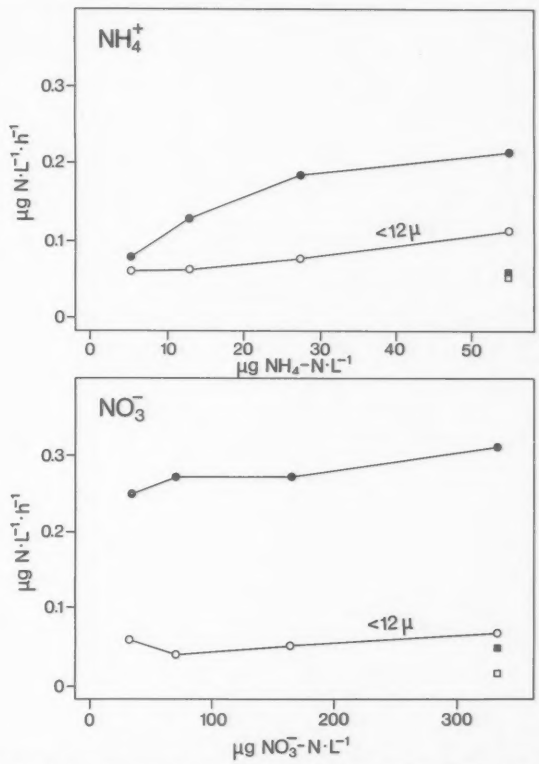

FIG. 8. Uptake rates for ammonium (top) and nitrate (bottom) as a function of added plus endogenous ammonium and nitrate. The uptake by all the plankton (solid symbols) is compared with that through 12 µm (open symbols). The experiment was conducted at 460 µEinst·m^{-2}·s^{-1} (circles) and in the dark (squares) at station 401 on 30 April.

dark ^{14}C-labeled bicarbonate uptake confirmed that most (approximately 70%) of the dark fixation is in the 0.2–1.0 µm fraction (Table 3).

Although the extracellular release of nitrite by phytoplankton, as suggested by Vaccaro and Ryther (1960), may occur, nitrification by chemoautotrophic bacteria can easily account for nitrite production. Ward (1984) cautioned, however, that the nitrapyrin method may overestimate nitrification and affect dark C assimilation by other bacteria and phytoplankton.

Nitrate and Ammonium Uptake Kinetics

Stable isotope ^{15}N-labeled nitrate and ^{15}N-labeled ammonium uptake measurements were conducted from 7 April to 20

TABLE 4. Variables for kinetic experiments.

Date	Station	Conditions	Temp. (°C)	NO_3^- ($\mu g N \cdot L^{-1}$)	NH_4^+ ($\mu g N \cdot L^{-1}$)	Particulate N ($\mu g N \cdot L^{-1}$)	Fig. ref.
30 April	401	Cold water	2.7	316	1	39	8
8 June	401	Thermal bar	10.1	280	2	65	10
10 June	403	Deep mixing	3.1	360	1	25	9
23 September	403	Stratification	16.3	130	10	70	11

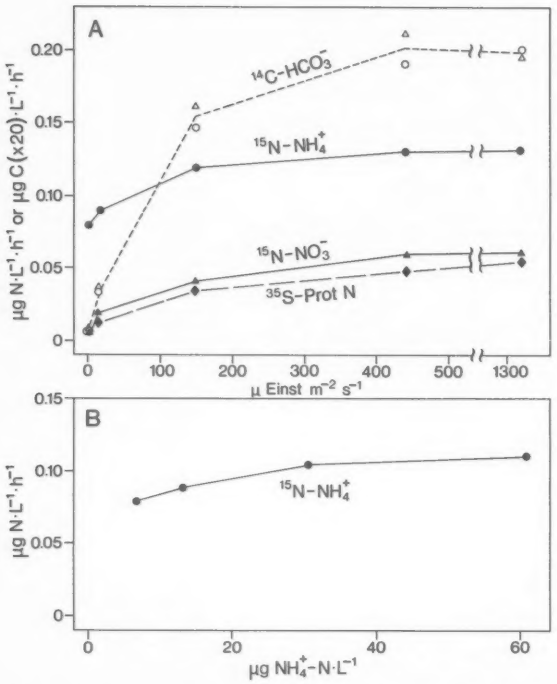

FIG. 9. (A) Ammonium (●) and nitrate (▲) uptake (solid lines), along with the corresponding C (broken line) uptake rates and ^{35}S-labeled protein-N (●) production as a function of light intensity. The experiment was conducted at station 403 on 10 June at added substrate levels of 66 and 333 μg N·L^{-1} for ammonium and nitrate, respectively. (B) Ammonium uptake velocity as a function of added ammonium at 150 μEinst·m^{-2}·s^{-1}.

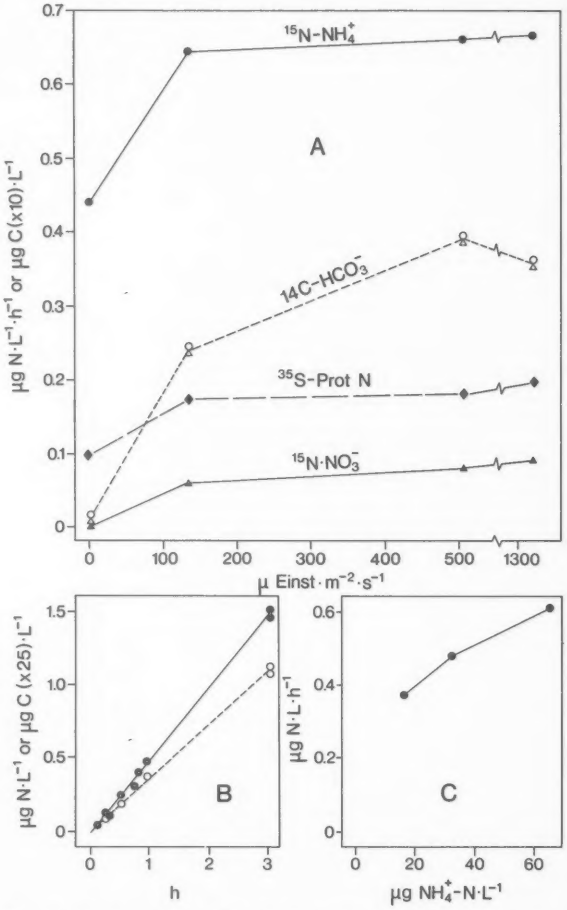

FIG. 10. (A) Ammonium (●) and nitrate (▲) uptake rates along with corresponding C (broken line) uptake rates as a function of light intensity. Experiment was conducted at station 401 on 8 June at added substrate levels of 66 and 333 μg N·L^{-1} for ammonium and nitrate, respectively. Also shown is the ^{35}S-labeled protein-N production. (B) Time course for ^{15}N-labeled ammonium (●) at 90 μg N·L^{-1} added substrate and corresponding C (○) uptake. (C) Ammonium uptake as a function of added ammonium at 150 μEinst·m^{-2}·s^{-1}.

November. Examples were selected to illustrate specific conditions: when the water was cold (Fig. 8, 9), when the nearshore was stratified (Fig. 10) but the midlake was still mixing (Fig. 9), and late summer stratification (Fig. 11). The experimental conditions are summarized in Table 4.

On several occasions, the uptake of nitrate and ammonium was measured on whole lake water and on water filtered through 12-μm Nuclepore filters after incubation. Unfortunately, these experiments were only conducted from April to the end of June (e.g. Fig. 8) but illustrate that small cells (<12 μm) were responsible for most of the ammonium uptake, especially at lower enrichments, while large cells used mostly nitrate. This partitioning precludes using any simple transformation to obtain half saturation coefficients. In the dark, almost all the ammonium uptake was by the <12 μm fraction and was equal to 27% of that at optimal light. Dark nitrate uptake by the <12 μm fraction was near zero, while that for whole lake water was 10% of that in optimal light. Certainly, these experiments must be repeated during summer stratification and in other lakes before generalizations can be made. Nevertheless, partitioning of the available

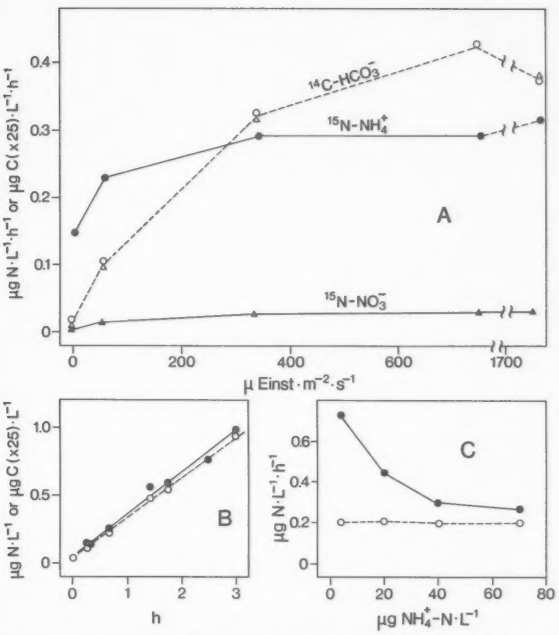

FIG. 11. (A) Ammonium (●) and nitrate (▲) uptake rates (solid line) along with the corresponding C (broken line) uptake rate as a function of light intensity. Experiment was conducted at station 403 on 23 September at added substrate levels of 40 and 400 μg $N \cdot L^{-1}$ for ammonium and nitrate, respectively. (B) Time course for ammonium and carbon uptake at 330 μEinst·$m^{-2} \cdot s^{-1}$. (C) Ammonium uptake shown as a function of added ammonium at 330 μEinst·$m^{-2} \cdot s^{-1}$ assuming that the ambient concentration is 10 μg $N \cdot L^{-1}$ as measured (●) or zero (○).

N seems to occur and is consistent with observations of Wheeler and McCarthy (1982) who showed that small cells (<1 μm) were responsible for much of the uptake of the ammonium analogue methylamine.

Common features of the uptake kinetics are illustrated in Fig. 9–11. It has been clearly established that ammonium is the preferred form of N for algal growth (e.g. Brown and Johnson 1977; McCarthy 1980). The elevated concentrations of nitrate resulted in uptake that was always near the maximal rate. Early in the season, the maximum uptake of ammonium was about equal to that for nitrate (e.g. Fig. 8). By 10 June, at 403, maximum nitrate uptake was less than maximal ammonium uptake (Fig. 9) for this deep mixing population. This pattern persisted, and in the September example, nitrate uptake was less than 10% of maximal ammonium uptake velocity (Fig. 11). Nevertheless, because ammonium was enriched much above ambient 1–3 μg $N \cdot L^{-1}$ concentrations, the contribution from nitrate at ambient concentrations would be much greater.

Ammonium and nitrate uptake, like ^{35}S-labeled sulfate uptake (Cuhel and Lean 1987b), reached optimal rates at lower light intensities than that for ^{14}C-labeled bicarbonate uptake and was not photoinhibited at high light intensities (Fig. 9–11). While dark nitrate uptake was often barely significant, dark ammonium uptake was 30–70% of that at optimal light.

Rates for protein synthesis (from Cuhel and Lean 1987a) using ^{35}S-labeled sulfate uptake were converted to protein N by assuming a weight percent N of 17 (Jukes et al. 1975). Early in the year, at 403, protein-N was equivalent to nitrate-N uptake, but at 401 under thermal bar conditions, some contribution from ammonium-N was required (Fig. 10). In the September example, no incubator measurements of protein synthesis were made, but values from in situ experiments were equivalent to nitrate-N uptake alone (Fig. 11). The advantage of the ^{35}S-labeled protein method (Cuhel and Lean 1987a, 1987b) is that sulfate is never stored and the concentration can always be easily measured. Instead of guessing which form of N is being used, protein synthesis can be reliably measured.

There has been a problem in marine systems involving initial rapid ammonium uptake rates (Goldman and Glibert 1982). To observe if this also occurred in Lake Ontario, time course experiments for ^{14}C-labeled bicarbonate and ^{15}N-labeled ammonium were run routinely throughout the entire period (e.g. Fig. 10B, 11B). Initial rapid uptake was not observed and the uptake of both forms was linear for periods of up to 4 h. This does not mean that the uptakes of bicarbonate and ammonium are necessarily coupled.

At station 403 on 23 September the maximal rates for ammonium and nitrate uptake were 0.32 and 0.03 μg $N \cdot L^{-1} \cdot h^{-1}$, respectively. The ammonium uptake curve had a very odd shape, i.e. less ammonium was taken up at high concentrations (Fig. 11C). This has been observed by other investigators (Toetz et al. 1973; Liao and Lean 1978) and even in Lake Ontario (Murphy 1980). The uptake curves approach those expected only by assuming that the measured ambient ammonium concentration was too high. This problem adds to the complexity of interpretation of ammonium uptake at ambient concentration.

The ammonium dark uptake rate was 0.15 μg $N \cdot L^{-1} \cdot h^{-1}$, (or 3.6 μg $N \cdot L^{-1} \cdot d^{-1}$, a value strikingly similar to the potential for nitrification using nitrapyrin-sensitive dark bicarbonate assimilation (Table 2). In nitrification, a great deal of ammonium must be oxidized to produce relatively little cell growth (Ward et al. 1982). This would leave nitrate uptake supporting much of the algal growth as postulated above.

Synthesis

The particulate nitrogen compartment (Fig. 12) contains algae, chemoautotrophic bacteria (CAB), and heterotrophic bacteria (HB), with some detritus. The contribution of major zooplankton to the particulate N compartment is relatively small and is shown separately. Unfortunately, present technology does not permit estimates of the relative contribution of each of these other forms. Even neglecting the contribution of microzooplankton and heterotrophic flagellates, zooplankton excretion has been shown to be a very significant process for ammonium regeneration (Fig. 5, 6; Table 2). Ammonium is oxidized by CAB (Fig. 7) and some nitrite accumulates as a result of this process (Fig. 1, 2). Nitrification in the deep water results in little accumulation of ammonium (Fig. 3, 4).

Much of the dissolved organic nitrogen (DON) may be colloidal (Wetzel 1981) and little progress has been made in the last 55 yr in characterizing the DON. With the exception of urea, noted by McCarthy (1980) and some amino acids, most of the DON must be biologically inert, for it changes little throughout the season (210 ± 16) and from year to year (Stevens and Neilson 1987).

N_2-fixation has been considered to be relatively insignificant when compared with the direct uptake of nitrite, nitrate, ammonium, and urea (McCarthy 1980). In Lake Ontario, there

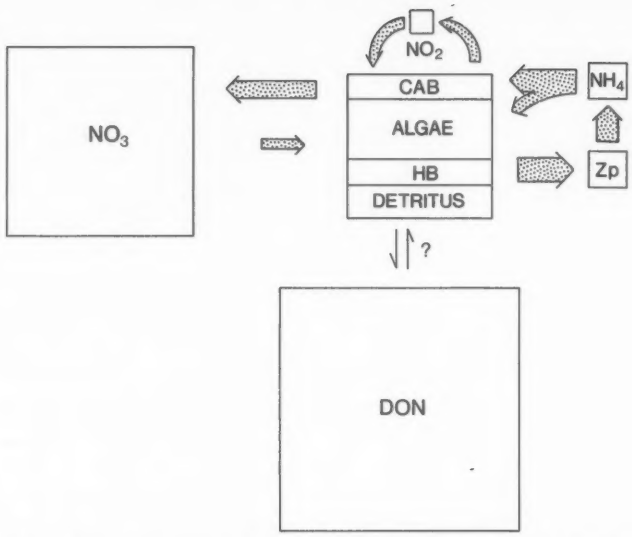

FIG. 12. Schematic model for integration of principal N transformations at station 403 on 23 September. Thickness of arrow denotes relative amount of N flux. Zooplankton (Zp) excretion represents a significant ammonium regeneration pathway. Utilization is partly by chemoautotrophic bacteria (CAB) with the production of nitrite and nitrate. Nitrate uptake is the principal source of N for algae. The role of heterotrophic bacteria (HB) is poorly understood as is the pathway between the particulate forms and dissolved organic nitrogen (DON).

were few N_2-fixing cyanobacteria (Gray 1987), and consequently, N_2 fixation was considered to be insignificant. Similarly, in view of the nitrous oxide profiles and the high oxygen concentrations (Fig. 5), denitrification was also thought to be unimportant. Instead, much of the "loss" in nitrate-N (Fig. 4) occurs when protein is transferred up the food chain to larger organisms not sampled in the present study.

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Photoinhibition of DCMU-Enhanced Fluorescence in Lake Ontario Phytoplankton

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Measurement of 1-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) enhanced fluorescence (F_{DCMU}) suggested that photoinhibition of photosynthesis was frequently an artifact of in situ bottle incubations in Lake Ontario phytoplankton. In a seasonal study, F_{DCMU} of all populations was depressed by bright light in an incubator. However, when the euphotic zone did not exceed the depth of the mixed layer, vertical transport of phytoplankton into either low-light or dark regions apparently allowed reversal of photoinhibition of F_{DCMU}. Advantages of F_{DCMU} as a bioassay of vertical mixing include rapidity of response time, ease of measurement in the field, and insensitivity of this parameter to changes in phosphorus status of the population. Because of seasonal changes in the photoadaptive response of natural populations, the rate constants and threshold light levels required to cause the response must be determined at each use if the method is to be quantitative.

Des mesures de la fluorescence augmentée par le DCMU (1-(3,4-dichlorophényl)-1,1-diméthylurée), désignée F_{DCMU}, indiqueraient que la photoinhibition de la photosynthèse est un artefact courant des expériences in situ d'incubation du plancton en bouteille réalisées dans le lac Ontario. Lors d'une saison d'étude, la F_{DCMU} de toutes les populations a été diminuée par une lumière vive en incubateur. Cependant, lorsque la zone euphotique n'excédait pas la profondeur de la couche de mixtion, le transport vertical du phytoplancton jusqu'aux zones de pénombre ou d'obscurité semblait donner lieu à une inversion de la photoinhibition de la F_{DCMU}. Les avantages de la F_{DCMU} dans la mesure de la mixtion verticale sont la rapidité, la commodité de la mesure sur le terrain et l'absence d'interférence due à la concentration de phosphore dans la population. À cause des changements saisonniers de la réponse photoadaptative des populations naturelles, les constantes de tuax et les intensités lumineuses seuils requises pour provoquer la réaction doivent être déterminées à chaque fois si on veut des résultats quantitatifs.

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Most techniques commonly used to measure photosynthesis in aquatic systems require incubation of samples in bottles for several hours to a day (Steeman-Nielsen 1952; Vollenweider 1974). "Photoinhibition" or the depression of photosynthesis at high light intensities both in situ and in simulated in situ incubators is often observed using this technique (Ryther 1956; Goldman et al. 1963; Vollenweider 1974; Knoechel and Kalff 1978; Gallegos et al. 1983; Goldman and Dennett 1984; Vincent et al. 1984). This effect was absent when phytoplankton were circulated through an irradiance gradient (Jewson and Wood 1975; Marra 1978), suggesting that during vertical mixing events, phytoplankton are only briefly exposed to high irradiances near the surface (Harris 1973a, 1973b, 1980; Harris and Piccinin 1977; Marra 1978, 1980). Photoinhibition may thus be expected only when the rate of vertical mixing is less than the time course of the onset of photoinhibition.

Photosynthetic carbon fixation requires ATP and reductant produced as a result of electron flow coupled through two photosystems (PSII and PSI) (Papageorgiou 1975; Crofts and Wraight 1983; Falkowski and Kiefer 1985; Prézelin and Boczar 1986). Photochemical processes are generally not measured directly in natural populations (but see Bates and Platt 1985; Demers et al. 1985). Fluorescence, a dissipative process during which a portion of the light energy absorbed by pigment molecules and transduced to PSII is reemitted, can be easily measured in situ without incubation. In vivo fluorescence is highly variable and is, to a large extent, regulated by thylakoid membrane state changes (Papageorgiou 1975; Lavorel and Etienne 1977; Falkowski and Kiefer 1985). The herbicide

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1-(3,4-dichlorephenyl)-1,1-dimethylurea (DCMU) binds the primary acceptor of PSII (Q_A), thus blocking electron flow between PSII and PSI (Izawa 1977; Crofts and Wraight 1983; Falkowski and Kiefer 1985). Under these conditions (and assuming dissipative processes other than fluorescence to be constant), fluorescence is enhanced since excitation energy arriving at PSII cannot be used for photochemistry.

Both in vivo and DCMU-enhanced fluorescence are rapidly depressed by exposure to bright light. It is believed that the photoinhibitory effects result from a combination of changes in ion flow, redox potential, thylakoid membrane state, energy distribution, and orientation of the chloroplast within the cell (Kok et al. 1965; Satoh 1970; Kiefer 1973b; Gerber and Burris 1981; Prézelin 1981). In nature, depression of both in vivo (Kiefer 1973a; Heaney 1978; Cullen and Renger 1979; Vincent 1979; Vincent et al. 1984) and DCMU-enhanced fluorescence (Cullen and Renger 1979; Harris 1980; Vincent et al. 1984; Elser and Kimmel 1985) in surface relative to deeper waters is likely a bright light response. Like photosynthetic carbon fixation, however, photoinhibition of F_{DCMU} may be altered by physical processes. Vincent (1980) observed a bimodal relation between F_{DCMU} and depth which he attributed to wind-driven Langmuir circulation. Harris (1980) did not observe surface depression of fluorescence in Hamilton Harbor when wind speeds were high and argued that active vertical mixing prevented cells from exposure to bright light at the surface of the water column long enough for photoinhibition of F_{DCMU} to occur. This result was confirmed by Elser and Kimmel (1985) in three southeastern United States reservoirs.

The question of whether DCMU-enhanced fluorescence could be used to indicate in situ photoinhibition of Lake Ontario phytoplankton was examined by comparing fluorescence properties of natural populations from three distinct physical regimes with those of the same populations incubated under constant light conditions.

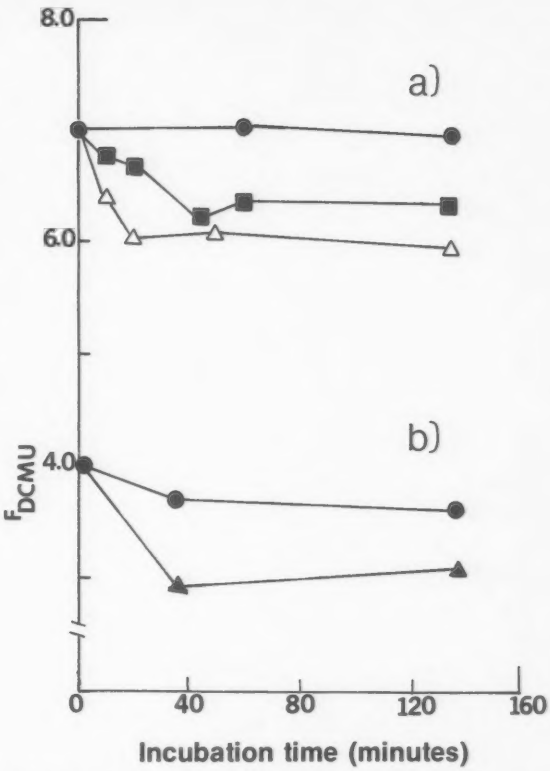

FIG. 1. Comparison of short-term changes in F_{DCMU} (relative units) incubated in constant light and in the dark. Samples were collected at 5 m on (a) 30 June and (b) 23 September and exposed to 1330 (△), 450 (■), and 430 $\mu E \cdot m^{-2} \cdot s^{-1}$ (▲) and to complete darkness (●).

Materials and Methods

Field work was conducted at two inshore (401, 405) and an offshore (403) station on Lake Ontario during cruises of the C.S.S. *Limnos* (Canada Center for Inland Waters) during 1982. Samples were collected in Niskin bottles and removed to the laboratory in white Nalgene jugs. Exposure to full sunlight was prevented: occasional comparisons of samples from Nalgene jugs and foil-wrapped containers showed no significant effect of the low irradiances inside the jugs on F or F_{DCMU}. In vivo fluorescence of chlorophyll *a* was measured using a Turner Designs model 10 fluorometer equipped with a red-sensitive photomultiplier. The filters and lamp were as recommended by the manufacturer (Blue lamp; excitation filter; Corning 5-60; reference filter; Corning 3-66; emission filter; Corning 2-64). The fluorometer was set to zero using 0.2-μm-filtered lake surface water. There were negligible seasonal differences between the standardization obtained with this water and with distilled water throughout the season. In vivo fluorescence (F) was measured on duplicate 25-mL subsamples within 15 min of subsampling the Niskin bottles. Twenty-five microlitres of DCMU was then added to obtain a final concentration of 1×10^{-5} *M* and a second fluorescence measurement (F_{DCMU}) was made after 10 min. Stock solutions of DCMU were dissolved in ethanol; addition of equivalent concentrations of ethanol to natural phytoplankton had no effect on F. Duplicate subsamples were also incubated in the dark at the in situ temperature for 1 h, following which F and F_{DCMU} were again determined. DCMU-enhanced fluorescence is expressed either in relative units per volume of water (F_{DCMU}) or per milligram of extracted chlorophyll *a* (F_{DCMU}/CHL). Error estimates ranged from 3 to 16% for F and 3 to 6% for F_{DCMU}. A difference between two numbers greater than twice the maximum error estimate (32% for F; 12% for F_{DCMU}) was considered significant.

For shipboard incubations, glass BOD bottles (300 mL) were rinsed three times, filled with lake water from 5 m, and placed on a rotating wheel at ambient temperature (±2°C). Light quality measurements are provided for the incubator in Cuhel and Lean (1987), and the light intensity and length of incubation for individual experiments are described in the text. Duplicate fluorescence measurements were made before and after each incubation as described above. For in situ incubations, glass BOD bottles were also filled with water sampled at depths to 20 m and the bottles resuspended at the same depth from which the samples were taken. F_{DCMU} was measured following incubations of 3–6 h and compared with profiles made in the water column prior to incubation. Although every effort was made to measure F_{DCMU} from the bottles within 15 min of removal from the site of incubation, this was often not possible and 30 min usually elapsed between collection of the incubated bottles and measurement of F_{DCMU}. Thus, these samples were in the dark for about 15 min longer than those sampled from the Niskin bottles. $H^{14}CO_3^-$ uptake was measured in the same samples

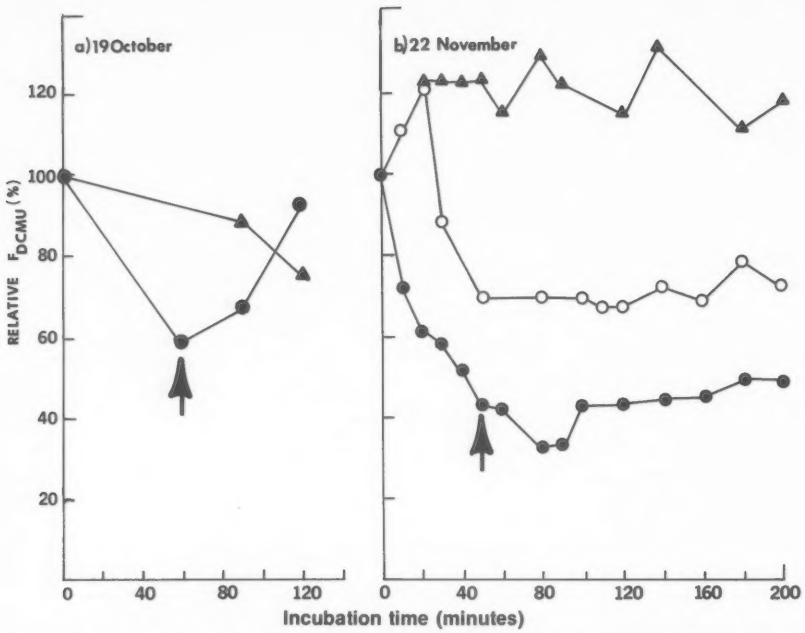

FIG. 2. Time course of change in F_{DCMU} for water collected at 5 m on (a) 19 October 1982 and (b) 22 November 1982 and incubated either in the dark (▲) (Fig. 2a, 2b) or at 1300 (●) (Fig. 2a), 470 (●) (Fig. 2b), or 150 $\mu E \cdot m^{-2} \cdot s^{-1}$ (○) (Fig. 2b). After 60 min. in the light, water samples were placed in the dark (indicated by arrow) and F_{DCMU} was measured for 1–2 h. F_{DCMU} expressed as F_{DCMU} at time t divided by the F_{DCMU} at t_0 multiplied by 100.

used for the fluorescence measurements according to the method of Lean and Burnison (1979). For determination of chlorophyll *a*, 100 mL of lake water was filtered onto GF/F filters, frozen, and later extracted using the hot DMSO/acetone method of Burnison (1980) for fluorometric analysis.

Solar radiation was determined from the pyrheliometer and water temperature measured using the bathythermograph aboard C.S.S. *Limnos*. The euphotic zone (z_{eu}) is the distance from the surface of the water to the 1% light level as measured near noon using a LiCor LI-185A quantum meter; the mixing depth (z_m) is the distance from the surface to the depth of maximum temperature change.

Results

F_{DCMU} but not F was a reliable indicator of previous exposure of phytoplankton to bright light. Depression of F_{DCMU} consistently followed incubation at high irradiances (Fig. 1, 2) whereas F did not always respond to bright light and was occasionally affected by incubation in the dark (data not shown). Hence, only the F_{DCMU}/CHL response will be described here. Incubations at light levels similar to those typically observed at 1 m in Lake Ontario during the summer (450–1330 $\mu E \cdot m^{-2} \cdot s^{-1}$) depressed F_{DCMU}/CHL within 10–30 min (Fig. 1, 2). In long-term incubations the magnitude of the response was clearly affected by light intensity (Fig. 3, 4). Following 3 h of exposure to irradiances of about 450–1330 $\mu E \cdot m^{-2} \cdot s^{-1}$, F_{DCMU}/CHL was consistently reduced by 30–81% compared with initial values and by 21–92% compared with dark-incubated samples. In contrast, $H^{14}CO_3^-$ uptake was frequently maximal at these intensities (Fig. 3). A comparison of diel time course measurements of F_{DCMU} and $H^{14}CO_3^-$ uptake yielded no apparent relationship (data not shown).

F_{DCMU}/CHL from deeply mixed spring and late fall samplings was clearly more susceptible to bright light depression than were summer samples, while no seasonal trend in the extent of photoinhibition of $H^{14}CO_3^-$ uptake in these incubations was obvious. From 10 June to 23 September, F_{DCMU}/CHL was not significantly depressed by incubation at irradiances <400 $\mu E \cdot m^{-2} \cdot s^{-1}$ and even at irradiances >1000 $\mu E \cdot m^{-2} \cdot s^{-1}$ F_{DCMU}/CHL was $>60\%$ of initial values (Fig. 3). However, in May and late October, incubation at light intensities near 300 $\mu E \cdot m^{-2} \cdot s^{-1}$ significantly depressed F_{DCMU}/CHL, with $>50\%$ reduction after incubation at >1000 $\mu E \cdot m^{-2} \cdot s^{-1}$.

For summer and early fall samples, depression of F_{DCMU}/CHL resulting from exposure to bright light was partially reversed by dark incubation. In a population exposed to light of 1300 $\mu E \cdot m^{-2} \cdot s^{-1}$ for 1 h followed by an 80-min dark treatment, F_{DCMU}/CHL returned to a level higher than that of cells maintained in constant dark (Fig. 2a). In day-long incubations an 8-h dark treatment always resulted in partial reversal of the light-induced depression (Fig. 4). Irreversible effects on F_{DCMU} in samples maintained in the light were only observed in November when depression of F_{DCMU}/CHL following as short as a 40-min incubation showed no change after a 2.5-h period in the dark (Fig. 2b).

Results of incubator experiments were used to interpret vertical profiles of F_{DCMU} for several stations with similarly high solar flux. Observations were made for three distinct types of water columns: (1) strongly stratified shallow (<5 m) epilimnetic water receving high irradiances (>400 $\mu E \cdot m^{-2} \cdot s^{-1}$) even at the bottom of the mixed layer ($z_{eu}/z_m >$

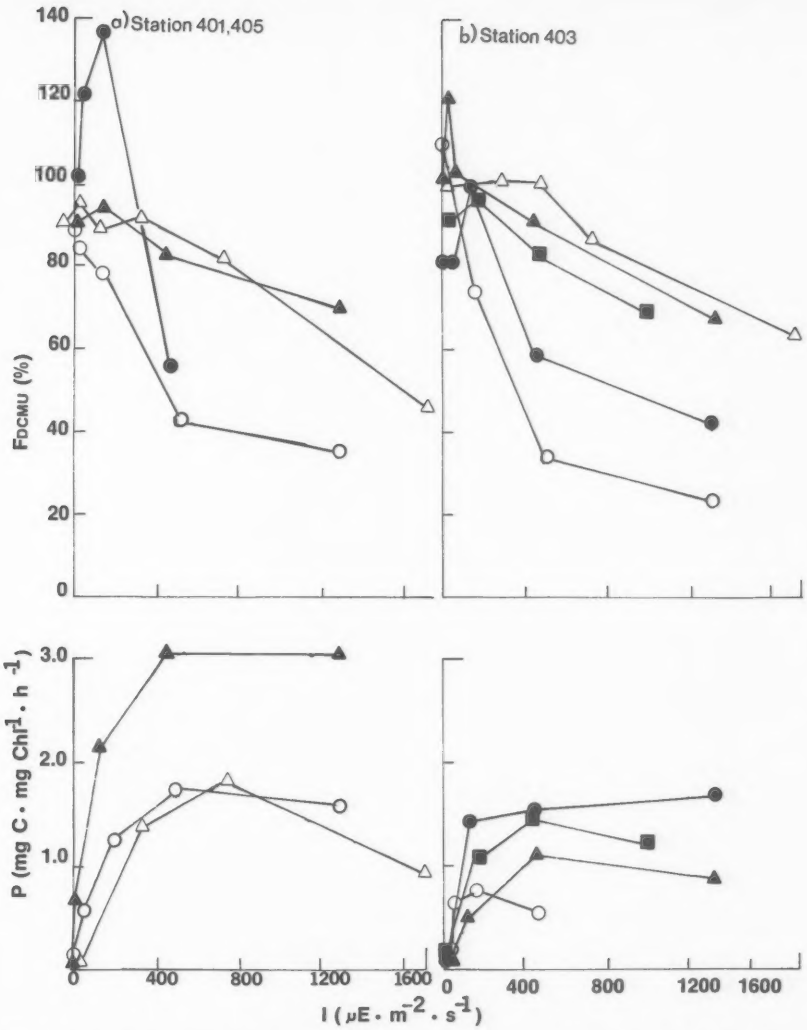

FIG. 3. Seasonal comparison of F_{DCMU} and ^{14}C uptake at different light intensities at (a) inshore stations 401 and 405 and (b) midlake station 403. Experiments were conducted on 18 May (●), 30 June (▲), 24 August (△), and 19 October (○) (Fig. 3a) and 18 May (●), 11 June (▲), 26 August (△), 23 September (■), and 22 November (○) (Fig. 3b). F_{DCMU} expressed as F_{DCMU} at time t divided by the F_{DCMU} at t_0 multiplied by 100.

1), (2) stratified water columns with a deep eipilimnion (approximately 10 m) where the bottom of the mixed layer received <40 $\mu E \cdot m^{-2} \cdot s^{-1}$ at midday ($z_{eu}/z_m = 1$), and (3) deep mixing of the water column before and after summer stratification ($z_{eu}/z_m < 1$) (Table 1).

In this study, in situ photoinhibition was documented only on 8 June at an inshore station (401) when the depth of the thermocline was <5 m and z_{eu}/z_m was >1 (Table 1; Fig. 5). On this day, subsurface irradiances exceeded 800 $\mu E \cdot m^{-2} \cdot s^{-1}$ for 7 h and the minimal light intensity to which phytoplankton circulating through the epilimnion were exposed exceeded 300 $\mu E \cdot m^{-2} \cdot s^{-1}$. At dawn, vertical profiles were homogeneous from the surface to 10 m with respect to F_{DCMU}/CHL (Fig. 5a). Subsequent in situ bottle incubations resulted in only slight depression of F_{DCMU}/CHL although surface rates of $H^{14}CO_3^-$ assimilation were about 30% less than those at 5 m (Fig. 5a). Surface depression of F_{DCMU}/CHL was more evident in a profile made at this time than at dawn (Fig. 5b). Midday incubation of this water at irradiances which consistently exceeded 1000 $\mu E \cdot m^{-2} \cdot s^{-1}$ at 1 m resulted in significant depression of both surface chlorophyll *a* specific photosynthetic rates and F_{DCMU}/CHL relative to maximal values observed at 7.5 m (Fig. 5b). Surface depression of F_{DCMU}/CHL was even more pronounced in a water column profile taken concurrent with removal of the bottles (Fig. 5c). By dusk (2100) there was reduction of photoinhibition in the water column although not in bottle-incubated samples which depicted similar strong maxima of F_{DCMU}/CHL and $H^{14}CO_3^-$ at 5 m (Fig. 5c).

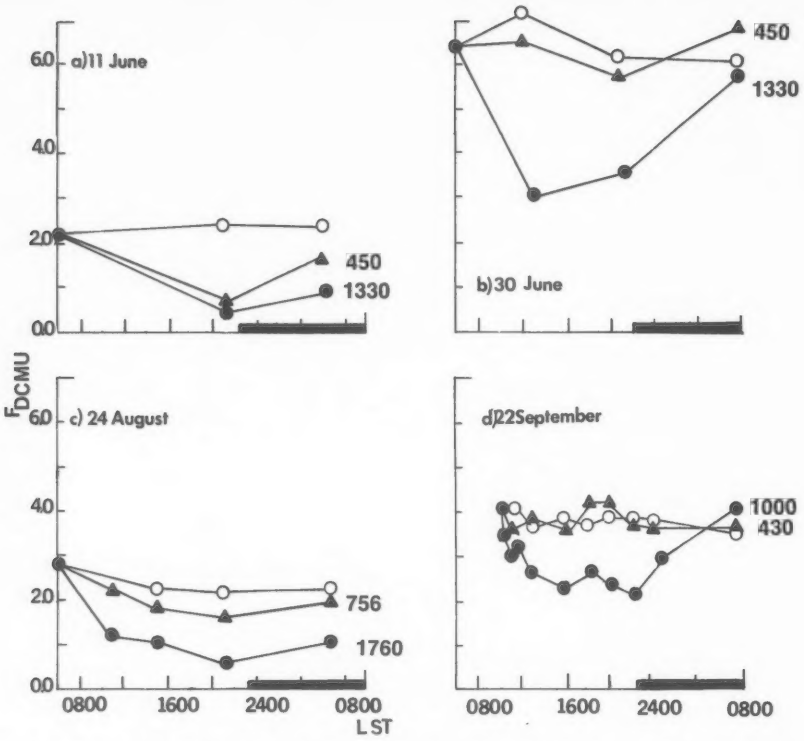

FIG. 4. Comparison of F_{DCMU} of samples incubated under artificial light in a light–dark cycle with those maintained in constant dark (black bar) for (a) 11 June, (b) 30 June, (c) 24 August, and (d) 22 September. Irradiances of incubation are shown.

TABLE 1. Physical data for Lake Ontario, 1982. Number of measurements in parentheses.

Date (station)	Mean wind speed (knots)	Thermocline depth (m)	1% I_0 (m)	z_{eu}/z_m	Number of hours irradiance >800 $\mu E \cdot m^{-2} \cdot s^{-1}$ at 1 m	Irradiance at thermocline ($\mu E \cdot m^{-2} \cdot s^{-1}$)	Maximum irradiance at 1 m ($\mu E \cdot m^{-2} \cdot s^{-1}$)
8 June (401)	4.3 (5)	5	13	2.6	7	183–438	1287
1 July (405)	10.4 (8)	10	11	1.1	7	10–19	1198
12 August (403	10.1 (7)	10	10	1.0	6	8–17	1158
26 August (403)	20.0 (1)	12	11	0.9	5	15–28	1036
22 September (403)	9.8 (4)	15	11	0.7	1	7–15	828

Two further observations were consistent with the hypothesis that subsurface maxima of F_{DCMU}/CHL resulted from photoinhibition of near-surface phytoplankton at midday. First, the in situ diel pattern of F_{DCMU} in water from 1 m on 8 June resembled that of water from 1 m maintained at constant light in an incubator on 11 June (Fig. 4a, 6a). On both occasions F_{DCMU} decreased throughout the day and recovered at night. This pattern was not observed in time course observations of water from 5 m (Fig. 6b). Secondly, increases in F_{DCMU}/CHL followed a dark incubation for midday 1-m samples (Fig. 6a), while little or no change occurred in dark-incubated samples from 5 m (Fig. 6b).

The importance of the depth of the mixed layer in restricting the duration of exposure to photoinhibitory irradiances was emphasized by experiments on 1 July and 26 August. On these occasions, light conditions in surface waters resembled those on 8 June (Table 1). In situ incubation lowered F_{DCMU}/CHL and produced moderate photoinhibition of chlorophyll *a* specific $H^{14}CO_3^-$ fixation at the surface (Fig. 7). In contrast with the June experiment, however, deepening of the thermocline to 10–15 m and moderately windy conditions enabled phytoplankton circulation through the mixed layer, with resultant exposure to much lower irradiances at the thermocline (<30 $\mu E \cdot m^{-2} \cdot s^{-1}$). Vertical profiles of F_{DCMU}/CHL for dawn, midday, and midafternoon on 1 July and 26 August were essentially homogeneous. Moreover, time course in situ studies showed no diel effects although the potential for bright light induced depression of F_{DCMU} in these populations was evident in incubator studies (Fig. 4b, 4c, 6c, 6d). There was also no effect of incubation in the dark (Fig. 6c, 6d).

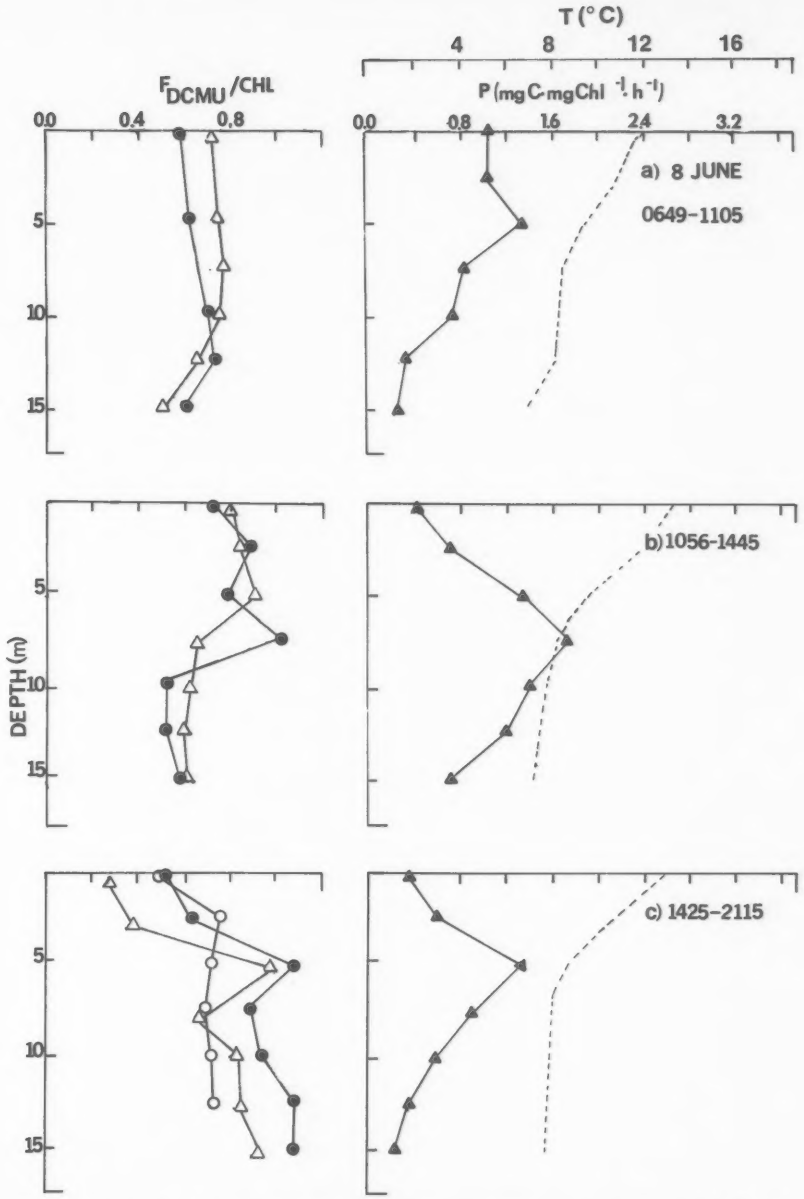

FIG. 5. Comparison of F_{DCMU}/CHL of water sampled directly from the water column prior to (△) and following (○) in situ incubation, F_{DCMU}/CHL of water incubated in bottles (●), and $H^{14}CO_3^-$ uptake (▲) at (a) 0649–1105, (b) 1056–1445, and (c) 1425–2115 on 8 June 1982. Temperature is indicated by a broken line.

The most extreme case occurred in spring and fall when the entire water column was isothermal and phytoplankton circulation was unrestricted by physical factors as on 22 September. In situ light levels were lower than in the summer (Table 1) but sufficient to cause slight photoinhibition of $H^{14}CO_3^-$ and F_{DCMU}/CHL in samples incubated in situ (Fig. 8). Constant artificial light incubation again resulted in a diel pattern of F_{DCMU}/CHL (Fig. 4d), but like the profiles from deeply mixed epilimnia, the water column was vertically homogeneous throughout the day (Fig. 8) and in situ F_{DCMU} showed no diel pattern.

Physical–biological interactions are summarized by a comparison of the relative difference in F_{DCMU} between 1 and 10 m (ΔF_{DCMU}) and the depth of the epilimnion (L) (Fig. 9). All

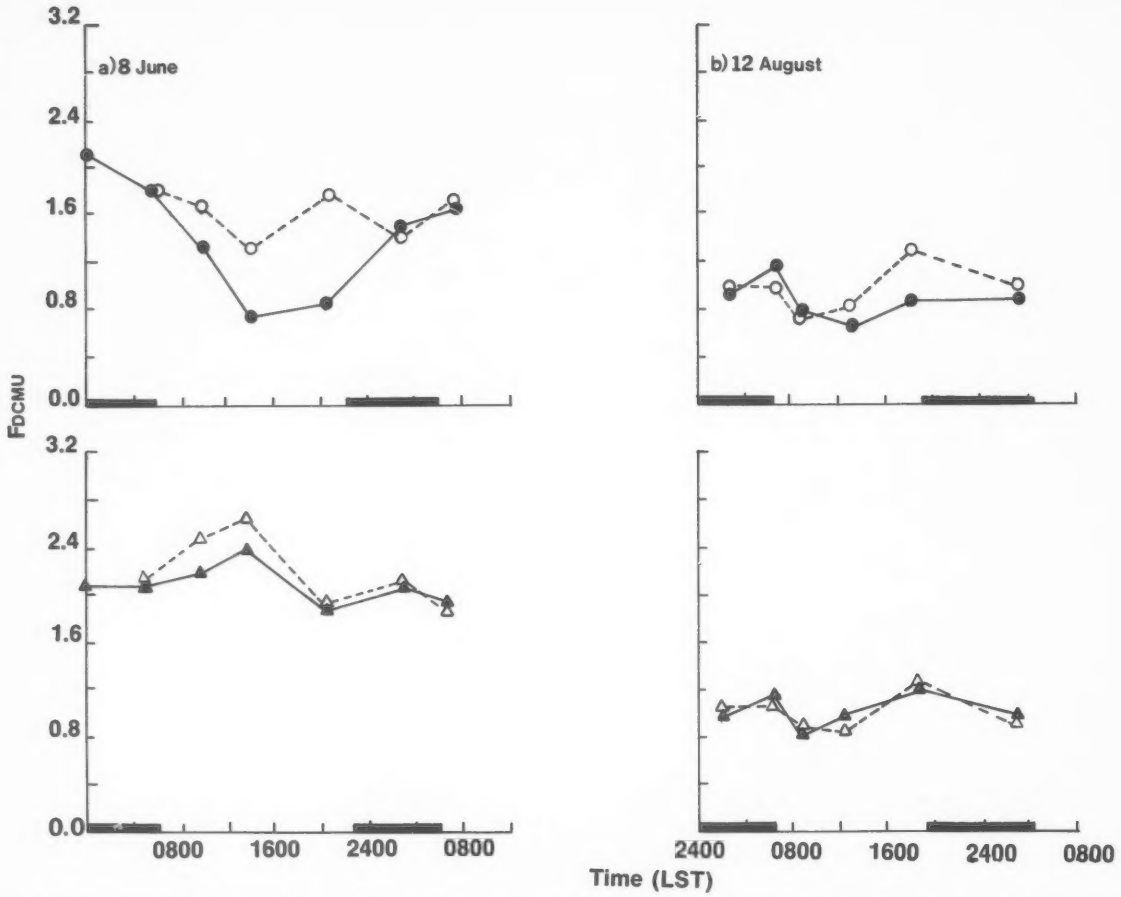

FIG. 6. Comparison of diel patterns of F_{DCMU} (relative units) in water collected from 1 (○) and 5 m (△) on (a) 8 June (station 403) and (b) 12 August (station 401) 1982. F_{DCMU} was measured immediately after incubation (●,▲) and again for subsamples held in the dark for a 1-h period (○,△).

profiles from 11 samplings over a 6-mo period, including those made at night and when light intensities were too low to affect F_{DCMU}, are presented. Hence, differences in F_{DCMU} between 1 and 10 m may have resulted from either photoinhibition of fluorescence or differences in the abundance of phytoplankton at the two depths. A shallow mixed layer did not consistently result in a difference in F_{DCMU} between 1 and 10 m (i.e. some low values of ΔF_{DCMU} were observed at low L), but the largest values of ΔF_{DCMU} were always observed in shallow mixed layers.

Discussion

In Lake Ontario a combination of physical and biological factors appeared to reduce the effects of photoinhibition on primary production. All populations tested showed the potential for becoming photoinhibited when incubated in a light–dark cycle at light levels representative of surface irradiances; however, the depth of the mixed layer appeared to be a critical factor in determing whether photoinhibition occurred in situ. When the depth of the mixed layer exceeded the depth of the euphotic zone, vertical transport of phytoplankton through the epilimnion into either low-light or dark regions apparently allowed reversal of photoinduced depression of F_{DCMU}. Phytoplankton circulating through an epilimnion where the depth of of the euphotic zone greatly exceeded the depth of the mixed layer received insolation for much of the day which was supraoptimal for photochemical and enzymatic processes. The latter situation likely only occurs during the spring in Lake Ontario at the onset of stratification. However, even on 8 June the shallow epilimnion which led to photoinhibition at the inshore station was restricted by the presence of a thermal bar (fig. 3 in Simons and Schertzer 1987). At this time of the year, much of the lake was isothermal and vertically homogeneous top to bottom. Elser and Kimmel (1985) observed near-surface photoinhibition in low-elevation temperate reservoirs but also suggested that vertical mixing likely limited its occurrence in situ. This situation contrasts tropical alpine Lake Titicaca where photoinhibition of F_{DCMU} was regularly observed as a result of the formation of near-surface thermoclines (Vincent et al. 1984).

A second aspect in the consideration of the impact of photoinhibition on primary productivity in Lake Ontario was the

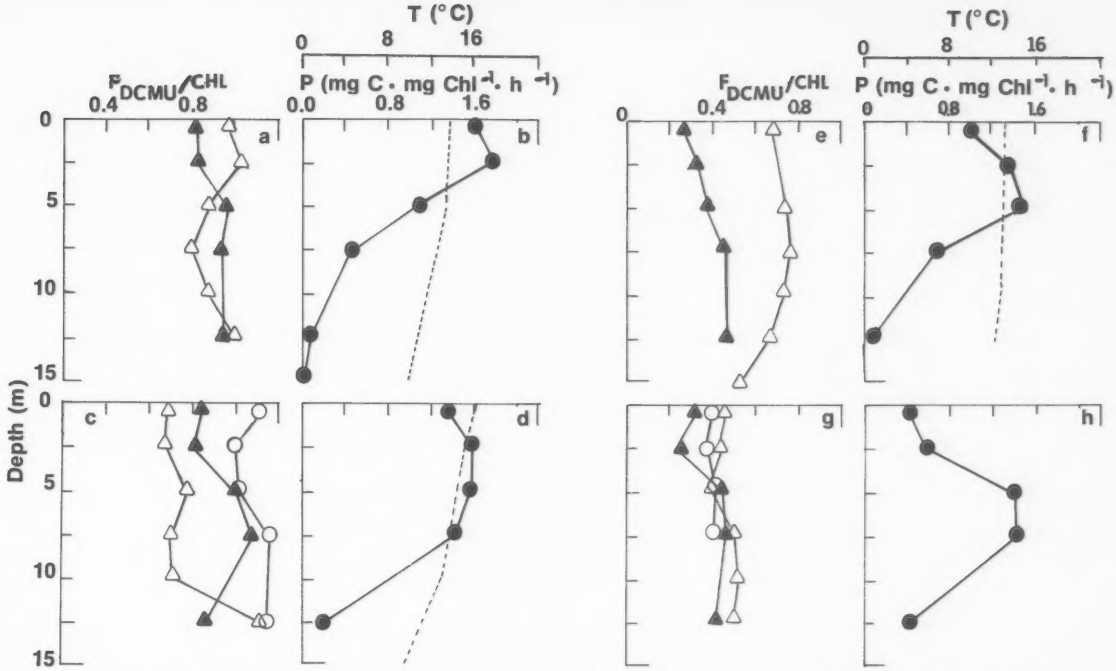

FIG. 7. Comparison of F_{DCMU}/CHL of water sampled directly from the water column prior to (△) and following (○) in situ incubation, F_{DCMU}/CHL of water incubated in bottles (▲), and $H^{14}CO_3^-$ uptake (●) at (a) 0555–1051 and (b) 1048–1540 on 1 July and (c) 0650–1050 and (d) 1055–1541 on 26 August. Temperature is indicated by a broken line.

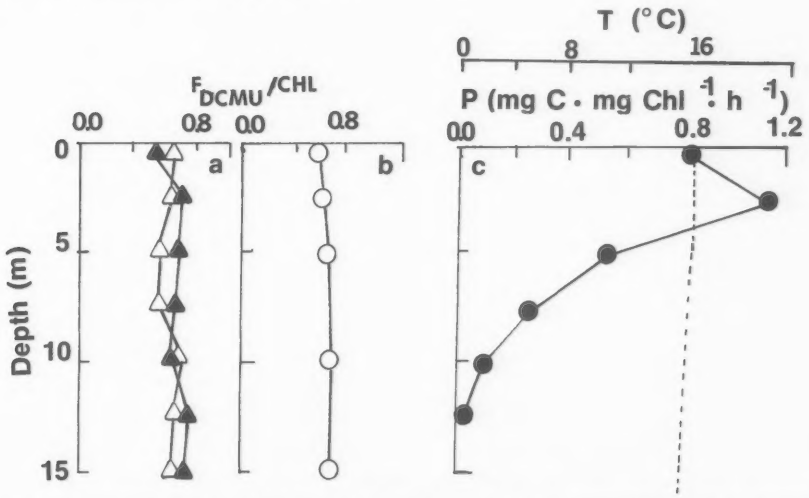

FIG. 8. Comparison of F_{DCMU}/CHL of water sampled directly from the water column prior to (△) and following (○) in situ incubation, F_{DCMU}/CHL of water incubated in bottles (▲), and $H^{14}CO_3^-$ uptake (●) at 0730–1750 on 22 September 1982. Temperature is indicated by a broken line.

decreased susceptibility of summer assemblages to photoinhibition of F_{DCMU}. Similar results have been observed for carbon fixation and oxygen evolution for both freshwater and marine systems and attributed in part to the predominance of diatoms or cryptomonads in the community (Harris 1973b; Tilzer and Schwarz 1976; Platt et al. 1980; Hobson and Hartley 1983; Goldman and Dennett 1984). Both of these taxonomic groups were present in Lake Ontario (Gray 1987) but their relative abundance was not correlated with susceptibility of the community to photoinhibition.

While some studies have shown good correlation between photosynthetic capacity and various indices of DCMU-

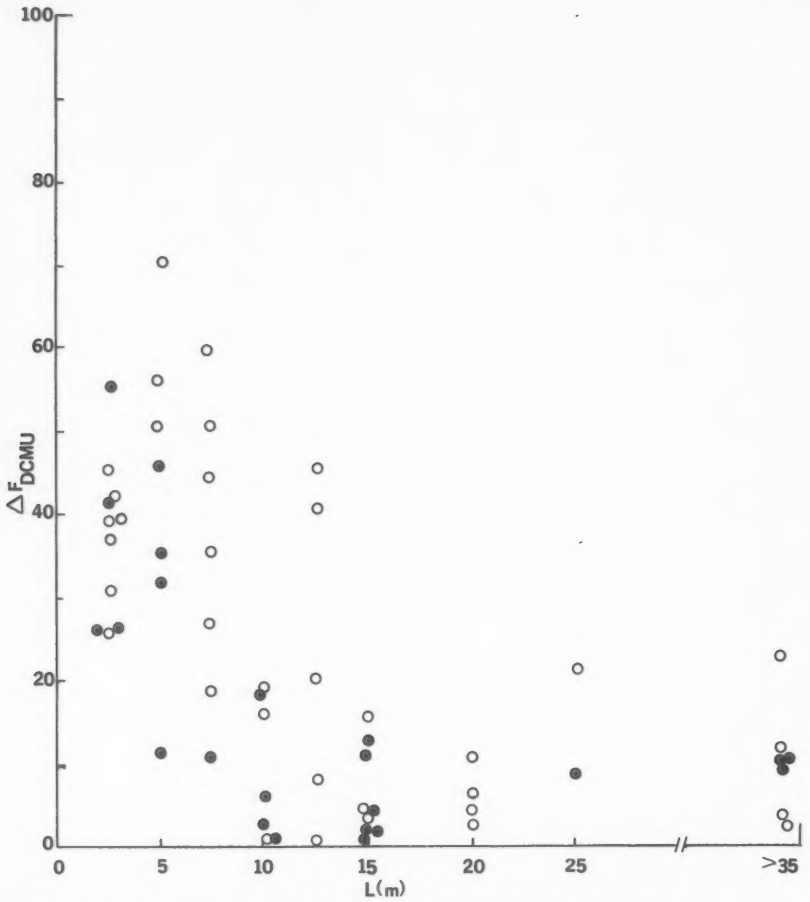

FIG. 9. Relationship of F_{DCMU} and depth of the epilimnion (L) between 1 and 10 m for 11 sampling occasions from 8 June to 22 November 1982. For the two depths, ΔF_{DCMU} is the difference in F_{DCMU} between 1 and 10 m. ● is from a profile made after sunset or before sunrise; ○ is from a profile made during the daylight hours.

enhanced fluorescence (Samuelsson and Oquist 1977; Roy and Legendre 1979; Prézelin and Ley 1980; Vincent 1980; Oquist et al. 1982; Vincent et al. 1984), we found no relationship between the two variables. This result is not unexpected for samples which have been incubated at high light intensities, since photoinhibition of fluorescence should be more rapid than photoinhibition of carbon fixation (c.f. Lewis et al. 1984). However, Droop (1985) also observed a great deal of scatter in the relationship between photosynthetic efficiency and a fluorescence index even in a unialgal culture at noninhibiting light intensities. The most reasonable conclusion is that the degree of correspondence between the two variables may be altered by environmental circumstances and physiological conditions (Prézelin 1981; Droop 1985; Falkowski and Kiefer 1985). In some cases in our study, a greater degree of photoinhibition of F_{DCMU} occurred in surface samples than in bottle-incubated samples (e.g. Fig. 6b, 6c). Photoinhibition has been shown to be a function of both light intensity and light quality. Ultraviolet radiation is most effective for inducing photoinhibition; however, glass bottles reduce the biologically effective dose at these wavelengths by up to 22% (Lorenzen 1979; Smith and Baker 1980; Hobson and Hartley 1983). Removal of bottles from the site of in situ incubation also took about 15 min longer than sampling from Niskin bottle casts. Thus, bottle-incubated samples received a longer period in the dark where reversal of photoinduced depression of F_{DCMU} could occur.

Recent studies have examined the utility of a suite of photoadaptive processes (including fluorescence, cellular chlorophyll levels, photosynthetic unit size, and photosynthesis–irradiance curves) as bioassays of vertical mixing (Falkowski 1980, 1983; Harris 1980; Lewis et al. 1984). In theory, if the rate of photoadaptation of some parameter exceeds the rate of vertical mixing, then that parameter will be nonuniformly distributed vertically. By examining a number of photosynthetic processes with different rates of photoadaptation, upper and lower bounds to the rate of vertical mixing are estimated (Lewis et al. 1984). Falkowski (1983) showed that the method required an estimate of the rate constants of photoadaptation for the measured parameter as well as measurements of the parameter at different depths in the mixed layer. Rate constants of

photoadaptation for cellular chlorophyll levels and photosynthetic unit size appeared to be reasonably estimated by a model incorporating first-order kinetics (Falkowski 1980, 1983). Data presented here (Fig. 1, 2) and previous studies (Kiefer 1973b; Vincent et al. 1984) suggested that a first-order model may also be appropriate for estimating rate constants for F_{DCMU}. Because of seasonal changes in the susceptibility of F_{DCMU} to photoinhibition, rate constants should be determined each time the assay is used. Of the various photosynthetic parameters measurable in the field, the rapid response time of F_{DCMU} makes it most suitable for systems where mixing rates are rapid. F_{DCMU} also has the advantage of being easily measurable. Furthermore, in Lake Ontario, where phosphorus is a major limiting nutrient to phytoplankton biomass, the addition of phosphorus prior to a 3-h artificial light incubation in five trials throughout a 7-mo period never resulted in a significant change in F_{DCMU} (data not shown). Thus, changes in fluorescence could be attributed to a change in the light field rather than the phosphorus status of the population.

The method is, however, obviously uninformative with respect to mixing rates on days when irradiance does not exceed the threshold level needed to illicit a photoinhibition response. Because F_{DCMU} is very sensitive to first-order variations in light (i.e. the absence of photoinhibition of F_{DCMU} may be due to passing clouds rather than turbulent mixing (Abbot et al. 1982; Falkowski 1983)), rate constants derived from field data will be most precise when in situ light is relatively constant.

In summary, F_{DCMU} proved to be a useful indicator of in situ exposure of phytoplankton to bright light. This information is potentially useful in determining when photoinhibition of photosynthesis occurs in situ and in estimating vertical mixing rates.

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Differences between Nearshore and Offshore Phytoplankton Communities in Lake Ontario

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Differences between nearshore and offshore phytoplankton biomass and composition were evident in Lake Ontario in 1982. Phytoplankton biomass was characterized by multiple peaks which ranged over three orders of magnitude. Perhaps as a consequence of the three times higher current velocities at the northshore station, phytoplankton biomass ranged from 0.09 to 9.00 $g \cdot m^{-3}$ compared with 0.10 to 2.40 $g \cdot m^{-3}$ for the midlake station. Bacillariophyceae was the dominant group at the northshore station until September when Cyanophyta contributed most to the biomass (83%). Although Bacillariophyceae was the principal component of the spring phytoplankton community at the midlake station, phytoflagellates (49%) and Chlorophyceae (25%) were responsible for summer biomass, with the Chlorophyceae expanding to 80% in the fall. The seasonal pattern of epilimnetic chlorophyll *a* correlated with temperature. While chlorophyll *a* concentrations were similar to values from 1970 and 1972, algal biomass had declined and a number of eutrophic species (*Melosira binderana, Stephanodiscus tenuis, S. hantzschii var. pusilla,* and *S. alpinus*) previously found were absent in 1982.

De nets écarts ont été notés, en 1982, entre la biomasse et la composition du phytoplancton des zones riveraines et du large du lac Ontario. La biomasse du phytoplancton se caractérisait par de nombreux pics présentant une gamme de variation de trois ordres de grandeur. La biomasse du phytoplancton notée à la station située au centre du lac variait de 0,10 à 2,40 $g \cdot m^{-3}$ tandis que celle notée à la station située sur la rive nord variait de 0,09 à 9,00 $g \cdot m^{-3}$, mais cela résulte peut-être du fait que le courant était trois fois plus rapide à cette dernière station. Les bacillariophycées ont été, jusqu'en septembre, le groupe dominant de la biomasse à la station nord, après quoi les cyanophytes représentaient la plus grande partie de la biomasse (83 %). Au printemps, les bacillariophycées étaient la principale composante de la communauté phytoplanctonique à la station située au centre du lac, mais les phytoflagellés (49 %) et les chlorophycées (25 %) constituaient la plus grande partie de la biomasse d'été; les chlorophycées en représentaient 80 % à l'automne. Le régime saisonnier de la chlorophylle *a* épilimnétique présentait une corrélation avec la température. Les concentrations de chlorophylle *a* étaient semblables à celles notées en 1970 et 1972, mais la biomasse de algues avait décliné et plusieurs espèces eutrophes (*Melosira binderana, Stephanodiscus tenuis, S. hantzschii var. pusilla* et *S. alpinus*), antérieurement présentes, étaient absentes en 1982.

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From 1974 to 1982, phosphorus loading, spring total phosphorus, and soluble reactive phosphorus declined in Lake Ontario whereas summer particulate organic carbon, nitrogen, and chlorophyll *a* showed no change (Stevens and Neilson 1987). The phytoplankton has been studied by Schenk and Thompson (1965), Michalski (1968), Nalewajko (1966, 1967), Reinwald (1969), Ogawa (1969), Screenivasa and Nalewajko (1975), and Stoermer et al. (1975), but only in 1970 (Munawar and Nauwerck 1971) and 1972 (Munawar et al. 1974) were the methods and station patterns sufficiently similar to permit comparison of seasonal patterns of phytoplankton biomass and composition. In 1970 a high percentage of diatoms were found at nearshore and offshore stations during the spring. Green algae and phytoflagellate were more dominant in the offshore region during the summer and fall. In 1972, phytoflagellates dominated the biomass at both nearshore and midlake stations for most of the year. Cryptomonads were more common at the northshore station and diatoms at the midlake station. Cyanophyta represented up to 30% of the total biomass in 1970 but were less important in 1972.

This paper describes the seasonal variation of phytoplankton biomass and its composition at a northshore and midlake station of Lake Ontario in 1982 compared with similar stations sampled in 1970 (Munawar and Nauwerck 1971) and 1972 (Munawar et al. 1974).

Materials and Methods

Phytoplankton biomass and species composition were investigated at two stations during 13 cruises on Lake Ontario between April and November 1982. Stations 401 and 403, located on a north–south transect across the lake (Simons and Schertzer 1987), were the northshore (38 m depth) and midlake stations (178 m), respectively. Sampling dates are listed in Tables 1 and 2.

Phytoplankton samples were taken from a water depth of 5 m using 6-L Niskin bottles on the rosette sampler of the CSS

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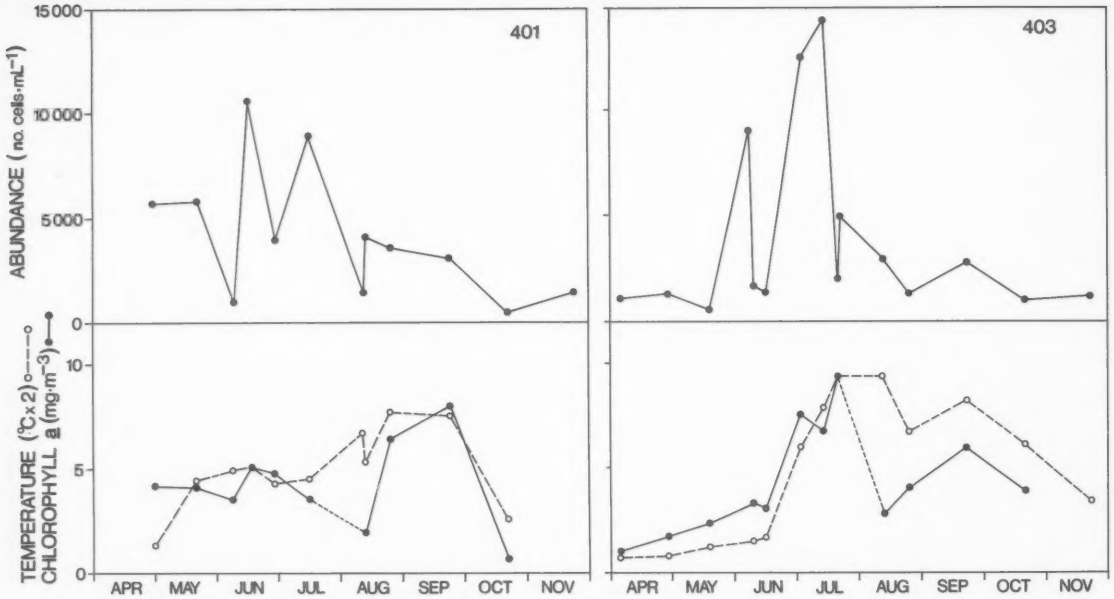

FIG. 1. Seasonal trends in temperature, chlorophyll *a*, and phytoplankton abundance at stations 401 and 403 in Lake Ontario, 1982.

Limnos. A sampling depth of 5 m was arbitrarily chosen as representative of the upper mixing zone. Samples were preserved with modified Lugol's solution (Nauwerck 1963; Vollenweider 1969) and phytoplankton were enumerated using the methods of Lund et al. (1958) which are based upon Utermöhl's (1931) techniques. Aliquots of 2–4 mL were sedimented in modified sedimentation chambers (Evans 1972) and examined on a Wild inverted phase-contrast microscrope at 400–1000×. The whole bottom area of the chamber was scanned for large or rare plankton using a low-power objective (200×). Generally between 50 and 200 units (cells, filaments, and colonies) of the taxa contributing most to total biomass were counted and measured. Total volume of each unit was calculated. Units without chloroplasts were not counted although few such units were noted. An enumerated sample totalled 200–800 units to achieve an adequate counting efficiency (Lund et al. 1958).

The cell volume of each species was computed from the average dimensions and the geometrical shape that most closely resembled the species form (Vollenweider 1969; Trevisan 1978). The total biovolume was recorded as total volume per millilitre. Biovolume was convered to wet weight assuming a specific gravity of 1.0.

Most commonly used taxonomic works for the identification of phytoplankton included Anton and Duthie (1981), Bourelly (1966, 1968), Germain (1981), Huber-Pestalozzi (1938–72), Prescott (1961), Taft and Taft (1971), and Skuja (1948, 1956, 1964). Phytoplankton samples are archived in the National Museum of Natural Sciences, Ottawa, Ont. (CANA 27772-27971).

Chlorophyll *a*, uncorrected for phaeophytin, was collected on Whatman GF/C filters and analysed by the Water Quality Branch, Burlington, Ont., following the methods of Strickland and Parsons (1972). Temperature was measured at each station with an electric bathythermograph.

Results

The seasonal pattern of chlorophyll *a* paralleled temperature (Fig. 1). In 1982 the northshore station (401) had stratified by late April with the thermal bar persisting until June (Simons and Schertzer 1987). At this time, chlorophyll *a* values ranged from 3.5 to 5.0 $mg \cdot m^{-3}$ as temperatures increased from 2 to 13°C. The midlake station (403) remained thermally homogeneous over the 178-m depth until the end of June. Chlorophyll *a* values increased from 1 to 3 $mg \cdot m^{-3}$ as temperatures warmed from 1 to 4°C. The main summer peak in July at station 403 occurred after the thermal bar spread over the lake at the end of June. Summer and fall chlorophyll *a* values ranged between 3 and 8 $mg \cdot m^{-3}$ at both stations.

In contrast with chlorophyll *a* concentrations, biomass fluctuated dramatically at stations 401 and 403 (Fig. 2) making the interpretation of "mean" biomass difficult. Nevertheless, station 401 had a mean biomass of 0.56 $g \cdot m^{-3}$ with a range of 0.09–9.29 $g \cdot m^{-3}$ in May. Even excluding the high value observed at station 401, station 403 had a slightly lower mean biomass (0.41 $g \cdot m^{-3}$) with a narrower range of 0.10–2.40 $g \cdot m^{-3}$ (Fig. 2).

The spring phytoplankton was composed mainly of Bacillariophyceae (68–79%) (Fig. 2). Over the season the northshore station had the highest mean percentage of Bacillariophyceae (40%). Chlorophyta and phytoflagellates constituted a greater mean percentage of the total biomass at the midlake station during the summer (24.8 and 48.8%, respectively). At the northshore station, Cyanophyta significantly contributed to the biomass (83%). At the midlake station during September, Chlorophyta significantly contributed to the fall peak in biomass (80%).

One hundred and seventy-four phytoplankton species were identified at the 5-m depths for the two stations in Lake Ontario. At the northshore station, significant contributions to the

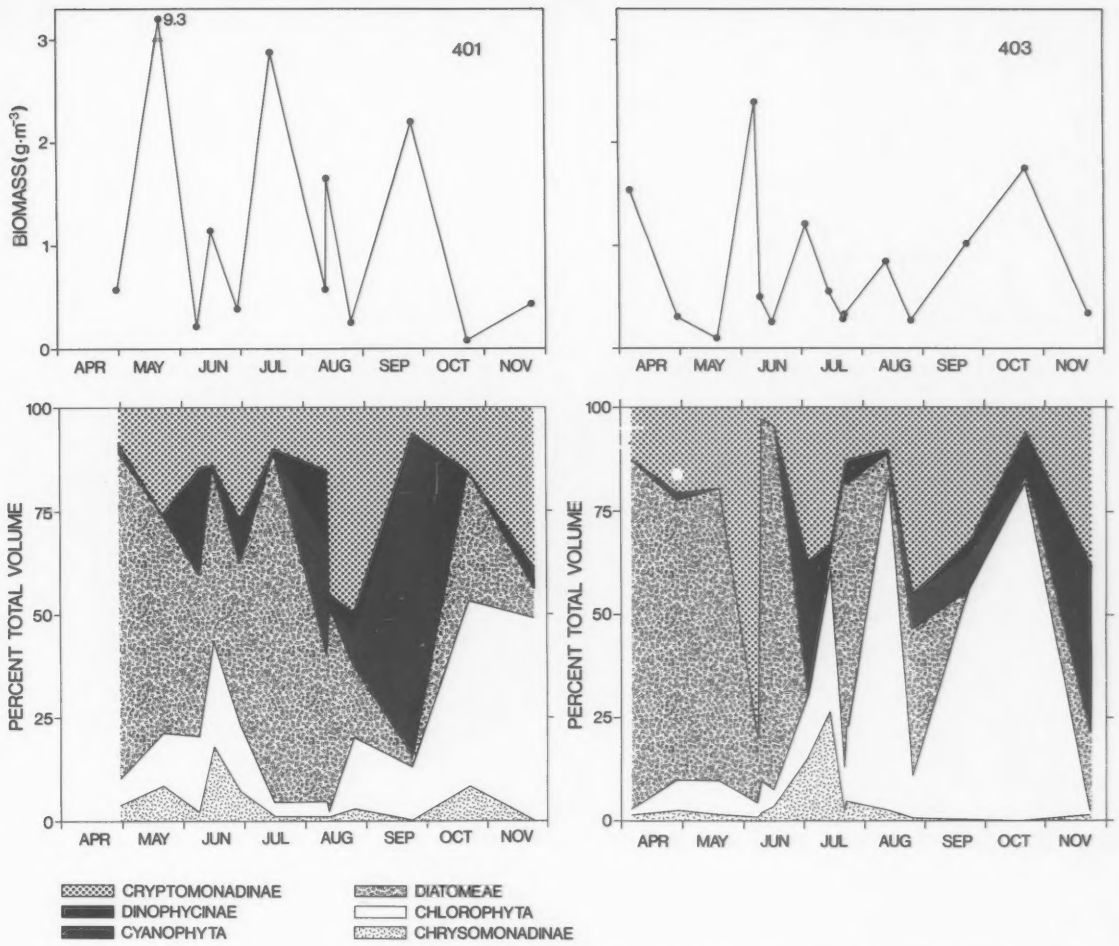

FIG. 2. Seasonal variations of 5-m phytoplankton biomass and its species composition at stations 401 and 403.

species succession were made by *Stephanodiscus hantzschii*, *Melosira islandica*, *Chrysochromulina parva*, *Tablellaria fenestrata*, and *Staurastrum* spp. (Fig. 3). Species persistent throughout the season included *Rhodomonas minuta*, *Asterionella formosa*, *Cryptomonas erosa*, *Chlamydomonas globosa*, and *Gymnodinium helveticum* (Table 1). Significant contributions to the species succession at the midlake station 403 included *Melosira islandica*, *Rhodomonas minuta*, *Chrysochromulina parva*, *Staurastrum paradoxum*, *Ceratium hirundinella*, and *Peridinium quadridens* (Fig. 4). Species persistent throughout the season included *Rhodomonas minuta*, *Cryptomonas erosa*, *C. ovata*, *Chlamydomonas globosa*, *Gymnodinium helveticum*, and *Scenedesmus bijuga* (Table 2). *Merismopedia* sp. was observed once at station 401 dominating the September sample. *Asterococcus* sp. dominated the early August sample at station 403 (Tables 1 and 2).

Diatoms dominant during the spring were different at the northshore and midlake stations: *Stephanodiscus hantzchii* at station 401 and *Melosira islandica* and *Tabellaria fenestrata* at station 403 (Tables 1 and 2). In the fall, Bacillariophyceae increased only at the northshore station (Fig. 2). *Tabellaria flocculosa* and *Stephanodiscus astrea* contributed to the biomass at the northshore station (Table 1).

Discussion

From the earliest reliable data of the mid-1960's, spring total phosphorus levels increased to about 23 μg $P \cdot L^{-1}$ by 1973 and then decreased to 14 μg $P \cdot L^{-1}$ in 1982, while summer total phosphorus and chlorophyll *a* have not shown any decreasing trend (Stevens and Neilson 1987). Midlake spring soluble reactive phosphorus and total phosphorus levels have decreased 33 and 42%, respectively, between 1973 and 1982, and with the increase in nitrate, the N:P ratio has increased from approximately 16 to greater than 35 since 1972 (Stevens and Neilson 1987). An increase in the TN:TP ratio has been shown to shift dominance from blue-green to green algae and diatoms (Smith 1986). Such dramatic changes in water chemistry should be

TABLE 1. Seasonal biomass of the most common species that contributed

Species	Apr. 29	May 20	June 8	Ju
Rhodomonas minuta Skuja	5.4	18.3	9.3	
Cryptomonas erosa Ehrenberg	—	—	—	
C. ovata Ehrenberg	—	—	—	
C. pusilla Bachmann	—	—	—	
C. reflexa Skuja	—	—	—	
C. rostratiformis Skuja	—	—	—	
Asterionella formosa Hassal	—	8.3	21.5	
A. gracillima (Hantzsch) Heiberg	—	—	—	
Melosira islandica O. Mueller	—	31.5	—	
Stephanodiscus astrea (Ehr.) Grunow	—	—	—	
S. hantzschii Grunow	68.8	8.0	—	
Synedra acus Kuetzing	—	—	—	
S. acus var. *angustissima* Grunow	—	—	12.3	
Tabellaria fenestrata (Lyngb.) Kuetzing	—	—	—	
T. flocculosa (Roth.) Kuetzing	—	—	—	
Ceratium hirundinella (O. Muell.) Dujardin	—	—	—	
Gymnodinium helveticum Penard	—	—	9.3	
Peridinium aciculiferum Stein	—	—	16.6	
Chromulina sp.	—	—	—	
Chrysochromulina parva Lackey	—	6.8	—	
Aphanocapsa sp.	—	—	—	
Merismopedia sp.	—	—	—	
Oscillatoria tenuis C. A. Agardh	—	—	—	
Carteria cordiformis (Carter) Diesing	—	—	7.0	
Chlamydomonas globosa Snow	—	—	—	
Chlamydomonas sp.	—	—	—	
Cosmarium reniforme (Ralfs) Archer	—	—	5.3	
Oocystis borgei Snow	—	—	—	
Pediastrum simplex var. *duodenarium* (Bailey) Rabenhorst	—	—	—	
Scenedesmus quadricauda De Brebisson	—	—	—	
S. bijuga (Turp.) Lagerheim	—	—	—	
Staurastrum chaetocerus (Schroeder) G. M. Smith	—	—	—	
Staurastrum paradoxum Meyen	—	—	—	

ıtributed 5% or more to the total phytoplankton biomass at station 401, Lake Ontario.

% of total volume									
ne 8	June 15	June 28	July 15	Aug. 11	Aug. 12	Aug. 24	Sept. 23	Oct. 21	Nov. 23
9.3	8.3	9.5	—	5.0	5.3	19.4	—	9.9	10.6
—	—	16.3	—	—	21.6	21.4	—	—	8.2
—	—	—	—	6.7	—	—	—	—	—
—	—	—	—	—	—	7.4	—	—	—
—	—	—	—	—	—	—	—	—	5.3
—	—	—	—	—	—	—	—	—	8.0
1.5	21.7	—	—	—	—	—	—	—	—
—	—	21.7	—	—	—	—	—	—	—
—	—	—	58.6	—	13.2	—	—	—	—
—	—	—	—	—	—	—	—	22.9	—
—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	8.7	—
2.3	—	—	—	—	—	—	—	—	—
—	—	7.1	8.5	32.8	34.9	14.6	—	—	—
—	—	—	11.0	—	—	—	—	—	—
—	—	—	—	15.1	—	—	—	—	—
9.3	—	11.2	—	—	—	—	—	—	—
6.6	—	—	—	—	—	—	—	—	—
—	—	6.7	—	—	—	—	—	8.2	—
—	14.4	—	—	—	—	—	—	—	—
—	—	—	—	27.6	—	—	—	—	—
—	—	—	—	—	—	—	74.8	—	—
—	—	—	—	—	—	8.9	—	—	—
7.0	—	—	—	—	—	—	—	—	—
—	18.7	—	—	—	—	—	5.4	—	—
—	—	—	—	—	—	12.9	—	—	—
5.3	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	10.8
—	—	—	—	—	—	—	—	—	15.5
—	—	—	—	—	—	—	—	18.4	—
—	—	—	—	—	—	—	—	13.4	—
—	—	—	—	—	—	—	—	—	13.8
—	—	—	—	—	—	—	5.6	—	—

TABLE 2. Seasonal biomass of the most common species that contributed 5% o

Species	Apr. 5	Apr. 28	May 18	June 7	June 9	June 15
Rhodomonas minuta Skuja	—	—	10.9	67.1	—	—
Cryptomonas erosa Ehrenberg	—	—	—	—	—	—
C. ovata Ehrenberg	—	—	—	—	—	—
C. pusilla Bachmann	—	—	—	—	—	—
C. reflexa Skuja	—	—	—	—	—	—
Asterionella gracillima (Hantzsch) Heiberg	—	—	—	—	—	—
Fragilaria crotonensis Kitton	—	—	—	—	—	—
Melosira islandica O. Mueller	—	60.3	65.4	—	79.9	45.4
Pinnularia sp.	—	—	—	—	—	6.0
Synedra acus var. *angustissima* Grunow	—	—	—	—	7.4	11.1
S. ulna (Nitzsche) Ehrenberg	—	—	—	—	—	12.9
Tabellaria fenestrata (Lyngb.) Kuetzing	75.8	—	—	—	—	—
Ceratium hirundinella (O. Muell.) Dujardin	—	—	—	—	—	—
Gymnodinium helveticum Penard	—	—	—	—	—	—
Gymnodinium sp.	—	—	—	—	—	—
Peridinium aciculiferum Stein	—	—	—	—	—	—
Chrysochromulina parva Lackey	—	—	—	—	—	—
Chroococcus dispersus (V. Keissler) Lemmermann	—	—	—	—	—	—
Oscillatoria tenuis C. A. Agardh	—	—	—	—	—	—
Asterococcus sp.	—	—	—	—	—	—
Carteria cordiformis (Carter) Diesing	—	—	—	—	6.7	—
Chlamydomonas globosa Snow	—	6.9	—	—	—	—
Chlamydomonas sp.	—	—	—	—	—	—
Cosmarium subnudiceps var. *granulatum* Taft	—	—	—	—	—	—
Oocystis borgei Snow	—	—	—	—	—	—
Staurastrum paradoxum Meyen	—	—	—	—	—	—

ed 5% or more to the total phytoplankton biomass at station 403, Lake Ontario.

	% of total volume									
9	June 15	July 2	July 13	July 20	July 21	Aug. 12	Aug. 24	Sept. 22	Oct. 20	Nov. 22
	—	11.7	18.9	—	—	—	11.1	—	—	19.3
	—	—	—	7.5	—	5.7	—	23.2	—	—
	—	—	—	—	—	—	32.3	—	—	10.2
	—	9.7	8.8	—	—	—	—	—	—	—
	—	5.8	—	—	—	—	—	—	—	—
	—	—	—	—	—	—	—	—	—	8.1
	—	—	—	—	50.4	—	—	—	—	—
	45.4	—	—	49.1	—	—	—	—	—	—
	6.0	—	—	—	—	—	—	—	—	—
	11.1	—	—	—	—	—	—	—	—	—
	12.9	—	—	—	—	—	—	—	—	—
	—	—	—	15.7	6.5	—	—	—	—	10.4
	—	—	—	—	—	—	—	—	8.9	—
	—	8.9	—	—	—	—	—	—	—	31.1
	—	22.8	—	—	—	—	—	—	—	—
	—	—	—	—	—	—	—	—	—	9.9
	—	6.8	23.4	—	4.7	—	—	—	—	—
	—	—	—	—	—	—	—	8.9	—	—
	—	—	—	—	—	—	9.1	—	—	—
	—	—	—	—	—	81.5	—	—	—	—
	—	7.9	11.9	—	—	—	—	—	—	—
	—	—	7.1	—	—	—	—	—	—	—
	—	—	5.0	—	—	—	—	—	—	—
	—	—	—	7.2	—	—	—	—	—	—
	—	—	—	—	—	—	—	38.2	—	—
	—	—	—	—	—	—	—	—	79.1	—

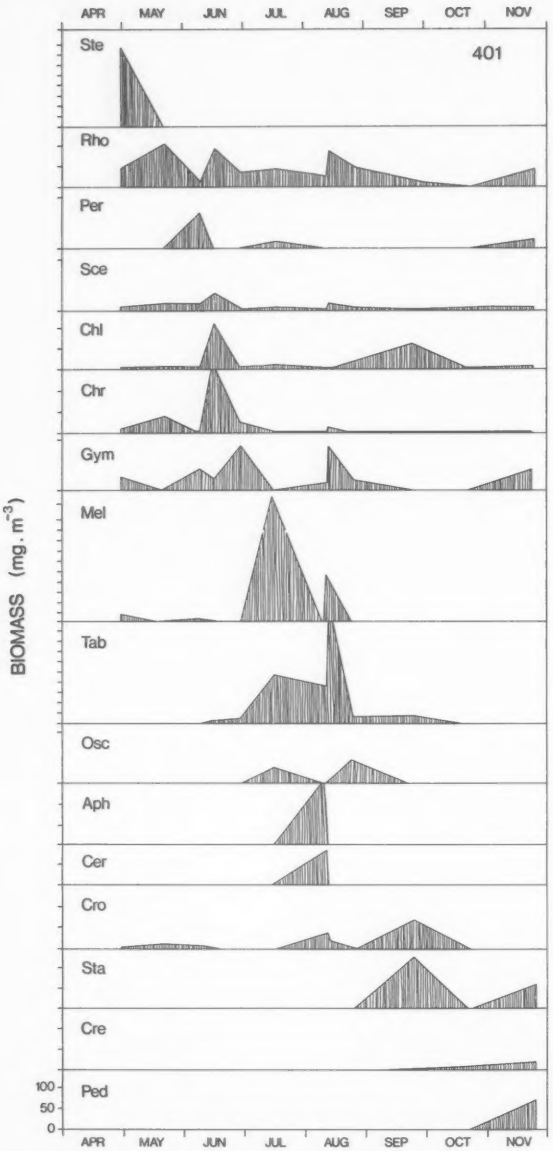

FIG. 3. Seasonal succession of species that contributed >5% to the total phytoplankton biomass at station 401. Ste = *Stephanodiscus astrea*, Rho = *Rhodomonas minuta*, Per = *Peridinium aciculiferum*, Sce = *Scenedesmus bijuga*, Chl = *Chlamydomonas globosa*, Chr = *Chrysochromulina parva*, Gym = *Gymnodinium helveticum*, Mel = *Melosira islandica*, Tab = *Tabellaria fenestrata*, Osc = *Oscillatoria tenuis*, Aph = *Aphanocapsa* sp., Cer = *Ceratium hirundinella*, Cro = *Cryptomonas ovata*, Sta = *Staurastrum* spp., Cre = *Cryptomonas erosa*, Ped = *Pediastrum* spp.

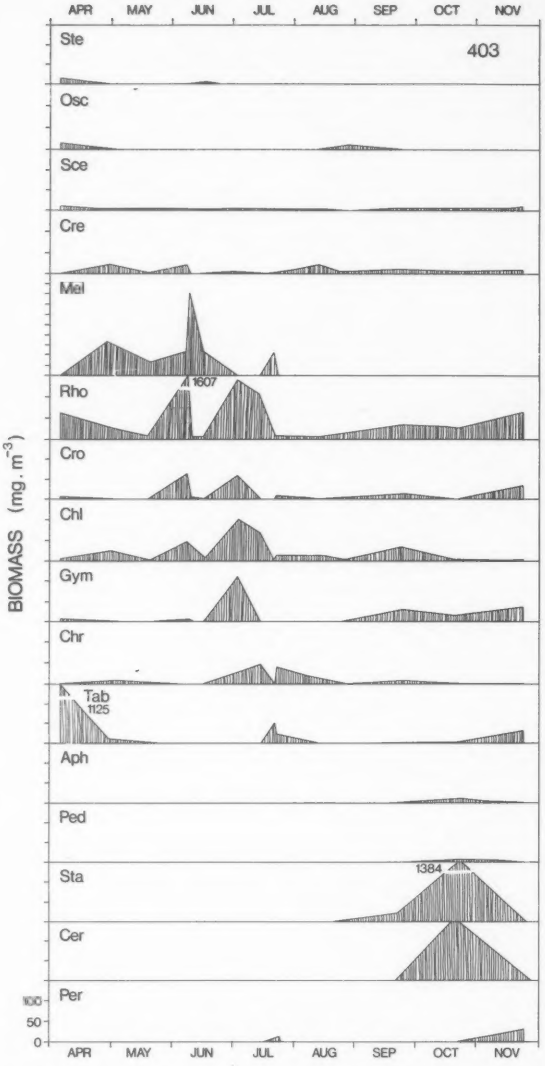

FIG. 4. Seasonal succession of species that contributed >5% to the total phytoplankton biomass at station 403. See Fig. 3 for abbreviations.

reflected in phytoplankton species composition and biomass. Differences were observed but may be complicated by other factors.

Slight differences in sampling methods existed but were not considered important. In 1970, biomass samples were collected at 1 and 5 m and mixed (Munawar and Nauwerck 1971). In 1972, samples were collected by a 0- to 10-m integrating sampler (Munawar et al. 1974). In 1982, a sampling depth of 5 m was chosen as representative of the upper mixing zone.

Despite the fluctuations in phytoplankton biomass, mean biomass was 43–58% less in 1982 than in 1972 (Table 3). A similar reduction was not observed for chlorophyll *a* values. Lack of correlation between chlorophyll and phytoplankton biomass values was evident in 1972 (Vollenweider et al. 1974) and 1982. While chlorophyll *a* data correlated well with water temperature ($n = 21$, $r = 0.63$, $p < 0.01$), biomass fluctuated with no consistent changes in chlorophyll *a* values ($n = 21$, $r = 0.28$, $p < 0.10$). Omission of a high biomass and low chlorophyll *a* values for station 401 ($9.2\ 10^3$ g·m^{-3} and 4.1 mg·m^{-3}, respectively) did not improve the relationship. In 1970

a phytoplankton biomass peak occurred during the summer at a time of chlorophyll minima (Munawar and Nauwerck 1971; Glooschenko et al. 1974). In 1972, chlorophyll *a* and phytoplankton biomass were correlated when data from a midlake and northshore station were combined (Stadelmann and Munawar 1974). When considering just the nearshore station, the relationship was weakened as a chlorophyll peak in early June did not coincide with the biomass peak in late June (Munawar et al. 1974). Similar discrepancies between phytoplankton biomass and chlorophyll *a* were observed in Lake Erie (Munawar and Munawar 1976). In Lake Superior, on the other hand, phytoplankton biomass and chlorophyll *a* showed a strong linear relationship which varied with season (El-Shaarawi and Munawar 1978). While it was suggested that the abundance of diatoms and phytoflagellates may have been responsible for the observed strong correlation, similar algal groups at the northshore station in 1982 did not result in a linear relationship ($n = 11$, $r = 0.28$, $p < 0.10$) between phytoplankton biomass and chlorophyll *a*. Chlorophyll *a* content per cell volume can vary markedly between species and thus contribute to discrepancies in yearly trends (Dolan et al. 1978; Lehman 1981). The lack of correlation between two biomass parameters, chlorophyll *a* and phytoplankton biomass, suggests serious implications when using either biomass parameter for predictive purposes. Discrepancies between chlorophyll *a* and phytoplankton biomass are beyond the scope of this paper, but further investigations should involve comparisons in phytoplankton enumeration using Utermöhl's and other methods.

Chlorophyll *a*/biomass ratios appear to have increased at the offshore stations in Lake Ontario between 1972 and 1982 (Table 4). Munawar et al. (1978) attributed differences in ratios between Lake Ontario and Lake Superior to the higher proportion of small-sized nanoplankton which contained more chlorophyll per unit biomass and which were most active photosynthetically. In midlake, the mean seasonal proportion of nanoplankton did not change between 1972 (Munawar et al. 1974) and 1982 whereas netplankton were less frequent in 1982 (unpublished data). There has also been a shift in dominant summer algal groups from blue-greens and greens in 1970 and phytoflagellates in 1972 to greens and phytoflagellates in 1982. Greens and cryptomonads contain more chlorophyll *a* per unit volume than diatoms and blue-greens (Reynolds 1984).

Prior to 1968 and before total phosphorus values were increasing (Stevens and Neilson 1987), phytoplankton abundances of northern nearshore waters of Lake Ontario exhibited a bimodal pattern with a well-defined spring maximum, lesser fall maximum, and definite winter minimum (Schenk and Thompson 1965; Michalski 1968). There was considerable variation in the frequency and periodicity of short, lesser pulses during the summer months (Schenk and Thompson 1965). In 1970 and 1972, peak biomass occurred during the high light, high temperature of the summer (Munawar and Nauwerck 1971; Munawar et al. 1974). The summer maximum developed earlier at the nearshore station but more irregularly than in the offshore region. In lakes where nutrients are never limiting, a single peak of phytoplankton biomass is not uncommon. The seasonal patterns for large unproductive lakes produce more predictable seasonal patterns although the timing of the peak biomasses may vary (Reynolds 1984). Physical limitations become dominant in nutrient-rich waters whereas nutrient availability limits less productive lakes producing biomodal biomass peaks during favorable physical conditions (Reynolds 1984). Now that phosphorus levels have declined since 1973, phytoplankton biomass of the two stations in Lake Ontario shows a bimodal pattern of biomass with a midsummer depression coming between a major spring peak and a lesser autumn peak, with short pulses occurring in the summer months.

TABLE 3. Total algal biomass and chlorophyll *a* concentrations for northshore and midlake stations on Lake Ontario during 1970, 1972, and 1982.[a] N/A = not available.

	1970	1972	1982
Biomass ($g \cdot m^{-3}$)			
Northshore			
Range	1–7	0.2–2.3	0.09–9.29
Mean	2.6	1.36	0.57
Midlake			
Range	<1–9	0.2–1.6	0.1–2.4
Mean	1.8	0.72	0.41
Chlorophyll *a* ($mg \cdot m^{-3}$)			
Northshore			
Range	5–6	1.9–8.0	0.6–8.0
Mean	N/A	4.96	3.2
Midlake			
Range	4–5	1.0–7.7	1.0–9.4
Mean	N/A	3.68	4.3

[a]1970 data calculated from Munawar and Nauwerck (1971); surface samples from a northshore station (station 40) and a midlake station (station 43). 1972 mean data calculated from Munawar et al. (1974); mean integrated samples (0–10 m) from a nearshore station (station 11) located near Oshawa and a midlake station (station 19). 1982 samples from 5-m depth at stations 401 (northshore located near Cobourg) and 403 (midlake).

TABLE 4. Comparison of chlorophyll *a*/phytoplankton biomass ratios for Lake Ontario.

Year	Location	Chlorophyll *a*/ biomass	Reference
1970	Whole lake	0.20	Munawar et al. 1978
1972	Nearshore (station 11)	0.36	Calculated from
	Offshore (station 19)	0.51	Munawar et al. 1974
1982	Northshore (station 401)	0.57	This study
	Midlake (station 403)	1.05	

Waters along the northern shores of Lake Ontario have been characterized by increased and variable phytoplankton biomass compared with the midlake region as a result of location, physical events, and nutrient loading (Nalewajko 1966, 1967; Munawar and Nauwerck 1971; Munawar et al. 1974; Haffner et al. 1984). In 1982, diatoms were dominant at a northshore station and greens and phytoflagellates at a midlake station. Inshore–offshore differentiation in biomass has also been reported for the central and eastern basins of Lake Erie (Munawar and Munawar 1975, 1976, 1981). Offshore stations were dominated by diatoms in the central basin and blue-greens in the eastern basin. Higher primary productivity, cell counts, and phytoplankton diversity occurred also in inshore regions of Lake Michigan (Schelske et al. 1971; Stoermer et al. 1971). Diatom populations were maintained at inshore stations, while blue-greens and greens were dominant at offshore stations. The upper Great Lakes, Lakes Superior and Huron (except Saginaw

Bay), had no well-developed inshore–offshore gradients (Munawar and Munawar 1975, 1981).

Species from Bacillariophyceae are often used as trophic indicators to differentiate inshore and offshore regions (Stoermer and Yang 1969; Munawar and Munawar 1980; Nicholls 1981). Nalewajko (1966, 1967) found nearshore stations to have a higher percent abundance of *Stephanodiscus tenuis*, while offshore stations had increased abundances of *Melosira islandica* and *Asterionella formosa*, indicating lower nutrient concentrations. During the winter to spring period of 1970, *Stephanodiscus tenuis*, *S. hantzschiii* var. *pusilla*, and *Melosira binderana* were found in large numbers at the inshore region and only in small numbers in the central region of Lake Ontario (Munawar and Nauwerck 1971). *Melosira islandica* ssp. *helvetica* dominated the offshore region. In 1972, *Melosira islandica* ssp. *helvetica* was dominant at both a nearshore and offshore station (Munawar et al. 1974). *Melosira binderana*, *Stephanodiscus tenuis*, *S. hantzschii* var. *pusilla*, and *S. alpinus* are all classified as mesoeutrophic indicator species and were all missing from the stations sampled in 1982. In the spring, *Melosira islandica* and *Stephanodiscus hantzschii* were dominant at the northshore station and *Melosira islandica* at the midlake station. *Tabellaria flocculosa* and *Stephanodiscus astreae* increased at the northshore station during the fall. *Tabellaria flocculosa* and *Melosira islandica* are considered oligotrophic species (Rawson 1956), while *Stephanodiscus hantzschii* is considered mesooligotrophic. While it is interesting to note that the two stations produced quite different species populations, the overall conclusion is that there has been a decline in eutrophic species.

Wind stress on the lake creates currents within the lake which alter the phytoplankton community and promote inshore–offshore differentiation. Boundary currents near the north shore were persistent throughout the season (Simons and Schertzer 1987). At the boundaries, surface velocities averaged 5–10 $km \cdot d^{-1}$ whereas at the midlake region, surface velocities averaged 0–4 $km \cdot d^{-1}$. The constant mixing of the nearshore area would tend to promote diatom growth and reduce their chances of sinking out of the phytoplankton community. An increase in larger plankton in areas of vertical mixing and/or upwelling is consistent with the views of Semina (1972), Malone (1980a, 1980b, and Harris et al. (1983).

The boundary currents were affected by a few summer storms. Only a few major wind events coincided with cruise dates (Simons and Schertzer 1985). During May 18–20 a major wind event occurred alongshore to create bottom currents just at the north and south shores. A major peak in phytoplankton biomass was measured at the northshore station consisting primarily of individual cells of *Melosira islandica* (Fig. 2; Table 1). The midlake station remained very calm with no change in the low level of biomass. The next northshore event to be monitored occurred on August 9 when all stations reacted to another large wind stress. In response, an upwelling occurred during August 10–11 at the northshore station. The temperature offshore was 18–20°C, while that at the northshore station was 10.6–13.4°C. During that time, the proportion of large plankton (>30 μm cryptomonads) increased at station 401 (Fig. 2). During fall turnover, increased winds and decreasing water temperatures promoted seeding and resuspension of large-sized plankton, *Merismopedia* colonies, and *Staurastrum paradoxum* at stations 401 and 403 (Tables 1 and 2).

In summary, physical events promote nearshore and offshore differentiation. Boundary currents persist throughout the season, intensified by a few summer storms which generally result in upwellings along the north shore. Biomass at the northshore station was 39% higher than at the midlake station, and multiple peaks were observed in spring and summer. Spring and fall maxima separated by lesser peaks during the summer were recorded at the midlake station. Compared with 1970 and 1972, the 1982 midlake and northshore stations have less algal biomass although chlorophyll *a* concentrations have remained unchanged. Diatoms dominated the phytoplankton population at the northshore station whereas greens and phytoflagellates dominated the population at the midlake station.

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Picoplankton and Nanoplankton Biomass in Lake Ontario: Relative Contribution of Phototrophic and Heterotrophic Communities

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The seasonal and vertical abundance of phototrophic and heterotrophic nanoplankton (2–20 μm) and picoplankton (0.2–2 μm) was estimated in Lake Ontario during 1982 by epifluorescence microscopy. Phototrophic and heterotrophic nanoplankton abundance differed by less than an order of magnitude and was typically present at densities of 10^3 cells·mL^{-1}. Heterotrophic nanoplankton was, on average, only half as abundant as phototrophic nanoplankton, but on several dates was more abundant than the latter. Both populations peaked in late June to early July. Phototrophic picoplankton, primarily chroococcoid cyanobacteria, increased rapidly during midsummer, reaching a maximum epilimnetic concentration of 4×10^5 cells·mL^{-1} in late August. Heterotrophic picoplankton (bacteria) showed a similar seasonal pattern, reaching maximum abundance in September (6×10^6) cells·mL^{-1}). The concentrations of both picoplankton populations were significantly correlated with temperature. By late summer, picoplankton biomass represented 74% and pico-cyanobacteria alone 50% of the total weight biomass of microorganisms <20 μm; these populations are generally missed by inverted microscope techniques.

L'abondance saisonnière et verticale du nanoplancton (2–20 μm) et du picoplancton (0,2–2 μm) phototrophes et hétérotrophes des eaux du lac Ontario a été estimée en 1982 par microscopie d'épifluorescence. L'écart entre l'abondance du nanoplancton phototrophe et celle du nanoplancton hétérotrophe était inférieur à un ordre de grandeur et les concentrations se situaient généralement au niveau de 10^3 cellules·mL^{-1}. En moyenne, l'abondance du nanoplancton hétérotrophe était de moitié inférieure à celle du nanoplancton phototrophe, mais il est arrivé à plusieurs occasions que le nanoplancton hétérotrophe soit le plus abondant. Les maximums des deux populations étaient notés entre la fin juin et le début de juillet. L'abondance du picoplancton phototrophe, surtout des cyanobactéries chroococcoidées augmentait rapidement à mi-été pour atteindre un maximum dans l'épilimnion de 4×10^5 celluls·mL^{-1} à la fin d'août. L'abondance du picoplancton hétérotrophe (bactéries) présentait un régime saisonnier semblable et atteignait son maximum en septembre (6×10^6 cellules·mL^{-1}). Les concentrations des deux populations de picoplancton présentaient une corrélation significative avec la température. À la fin de l'été, la biomass du picoplancton représentait 74 %, et celle du picoplancton-cyanobactéries représentait à elle seule 50 %, de la biomasse totale (poids humide) des microorganismes < 20 μm. L'existence de ces populations passe généralement inaperçue à l'examen microscopique par inversion.

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Our understanding of the types and densities of microbial plankton populations has evolved gradually as a result of improvements in sampling and enumeration techniques. The first field studies of freshwater and marine planktonic microorganisms were based on samples collected with plankton nets of relatively coarse mesh (e.g. Gran 1912; Ruttner 1963). These early studies demonstrated the diversity and abundance of the larger phytoplankton (netplankton). Subsequent application of inverted microscope techniques (Utermöhl 1931) increased our knowledge by drawing attention to the smaller algae (nanoplankton) which often dominate total phytoplankton biomass and productivity (e.g. Gliwicz 1967; Malone 1971; Kalff 1972; Munawar and Munawar 1975). Unfortunately, the term nanoplankton has not been consistently defined and varies from microorganisms passing a 10-μm screen (McAllister et al. 1959) to those passing a 64-μm screen (Yentsch and Ryther 1959; Munawar et al. 1974). However, the definition of Dussart (1965) for

microorganisms between 2 and 20 μm, based on a logarithmic scale, is gaining wider acceptance (Sieburth et al. 1978; Malone 1980).

The application of epifluorescence microscopy to the study of planktonic microorganisms has enabled the accurate determination of bacterial densities in the picoplankton size class (0.2–2 μm) (Hobbie et al. 1977; Watson et al. 1977). These estimates are much greater than estimates from traditional procedures (Jannasch and Jones 1959). More recently the technique resulted in the discovery of phototrophic microorganisms in the picoplankton size class. These phototrophs are distinguished from the heterotrophic bacteria by the autofluorescence of photosynthetic pigments. In marine systems this population consists largely of chroococcoid cyanobacteria and minute eukaryotic algae (Johnson and Sieburth 1979; Waterbury et al. 1979; Johnson and Sieburth 1982). Primary production studies have confirmed their importance in marine communities (Li et al. 1983; Platt et al. 1983). Their importance in freshwater systems is less well-characterized, but high population densities of pico-cyanobacteria have been found in several lakes (Lehman and Sandgren 1982; Craig 1984; Sicko-Goad and Stoermer 1984; Caron et al. 1985). Collectively these studies indicate that most of the primary production formerly attributed to the nanoplankton and a substantial part of the total planktonic primary production may be due to the activity of the picoplankton.

Epifluorescence microscopy has also been adapted in marine planktonic communities to distinguish the phototrophic (Pnano) and heterotrophic (Hnano) components of the nanoplankton by using the autofluorescence of chlorophyll *a* as a diagnostic tool (Davis and Sieburth 1982; Haas 1982; Caron 1983; Sherr and Sherr 1983). Davis and Sieburth (1982) have demonstrated that estimates of heterotrophic nanoplankton densities determined by epifluorescence microscopy are significantly greater than estimates by the Utermöhl tecnnique, indicating a greater contribution of these microorganisms to the biomass of planktonic communities than was previously believed. The generalization emerging from these studies is that roughly one half of the microorganisms composing the nanoplankton, formerly thought to be predominantly or solely phototrophic, are heterotrophic. Heterotrophic flagellates and ciliates of the nanoplankton are now considered to be the primary consumers of the picoplankton in the oceans (Fenchel 1982; Azam et al. 1983) and may be important in the remineralization of nutrients (Caron et al. 1982; Sherr et al. 1982). However, relatively little is known about their importance in freshwater.

As part of a larger study conducted in 1982 on energy and nutrient cycling in Lake Ontario, we determined the seasonal and spatial distribution of picoplankton and nanoplankton at three stations. To our knowledge, the following represents the first quantification of the relative biomass of phototrophic and heterotrophic nanoplankton and picoplankton in a freshwater system.

Methods and Materials

Lake Ontario water samples were collected from stations 401 (north shore, 43° 53′ 29″, 78° 15′ 44″), 403 (midlake, 43° 35′ 52″, 78° 13′ 51″), and 405 (south shore, 43° 24′ 03″, 78° 12′ 00″) from April through November 1982 with the rosette sampler of the CSS *Limnos*. These stations are described in Lean (1987). Sterilized bottles were filled with water from selected depths, and glutaraldehyde buffered with 0.1 *M* sodium cacodylate at pH 7.2 was added at a final concentration of 1.0% v/v. Preserved samples were maintained at 4°C in the dark. Counts of the picoplankton and nanoplankton were performed within 48 h, but in some cases, microscopical examination was delayed for up to 12 d. We observed no significant change in the number of autofluorescent cells during this period.

Enumeration was done by epifluorescence microscopy using a Zeiss standard microscope equipped with a 50-W or 100-W HBO mercury lamp (Caron et al. 1985). Photosynthetic picoplankton (Ppico), photosynthetic nanoplankton (Pnano), and heterotrophic nanoplankton (Hnano) were counted by autofluorescence using a BP450-490 exciter filter, an FT510 chromatic beam splitter, and an LP520 barrier filter. Slides were prepared by gently (<14 kPa vacuum pressure) filtering 10–25 mL of preserved lake water through 0.45-μm Millipore filters. These were dried at 60°C for 15 min and then cleared with Cargill A low-fluorescence immersion oil. On most occasions, preserved samples were also filtered through prestained Nuclepore filters for enumeration, as described in Caron et al. (1985), to ensure that the drying step did not quench chlorophyll fluorescence thereby resulting in lower counts of photosynthetic cells. The Nuclepore filters, however, do not give as good a visualization of heterotrophic flagellates.

Under these conditions, the autofluorescent picoplankton of Lake Ontario was dominated by yellow to orange fluorescing cells which is indicative of cyanobacteria (described by Caron et al. 1985). The presence of the biliprotein pigment phycoerythrin masks the intense red autofluoresence of chlorophyll *a*. Non-phycoerythrin-containing cyanobacteria require more involved techniques of enumeration (e.g. Campbell et al. 1983) but these were not numerous in Lake Ontario although they can predominate in softwater lakes (F. R. Pick, unpubl. data). Cryptomonads, which are an important component of Lake Ontario phytoplankton (Munawar and Nauwerck 1971; Gray 1987), fluoresce an orange–red due to the presence of phycobiliproteins. However, the latter groups cannot be confused because cryptomonads are flagellated and > 2 μm diameter. Heterotrophic nanoplankton fluoresce a dull green. Although this procedure for counting nanoplankton is more tedious to perform than fluorochrome staining techniques commonly employed (Davis and Sieburth 1982; Caron 1983: Sherr et al. 1982), it proved to be more useful in Lake Ontario due to the presence of varying amounts of particulate material which absorbed the stain and obscured the nanoplankton.

Scans across the filter were examined at 1000×, and only organisms < 20μm in size were counted. Larger algae and ciliates were enumerated by Gray (1987) and Taylor and Heynen (1987), respectively. Over 400 pico-cyanobacteria and between 75 and 100 of both Hnano and Pnano were counted on each prepared slide. Dimensions of each cell type were measured to calculate average volumes. Biovolume was calculated by multiplying the number of cells per millilitre of each type by the calculated volume. Wet weight biomass conversions were made by assuming a specific gravity of 1.

Heterotrophic picoplankton (Hpico, bacteria) were counted using the fluorescent dye DAPI (4′,6-diamidino-2-phenylindole) (Porter and Feig 1980) with a final stain concentration of 1.0 $\mu g \cdot mL^{-1}$. The Nuclepore filters (0.22 μm pore size) were prestained with Irgalan black rather than Baker black. A G365 exciter filter, an FT420 chromatic beam splitter, and an LP418 barrier filter were used for the bacterial counts. Over 600

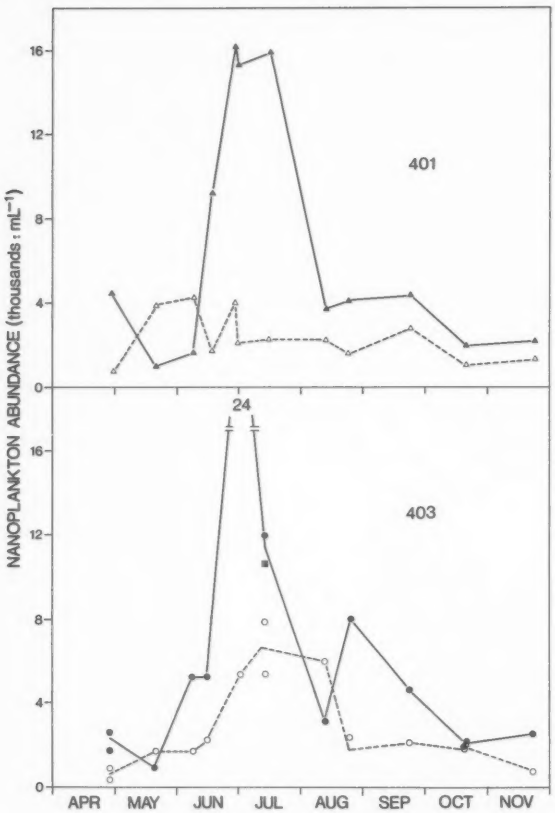

FIG. 1. Abundance of photosynthetic (dark symbols) and heterotrophic (open symbols) nanoplankton (2–20 μm) at 5 m in Lake Ontario during 1982. Upper panel: station 401 (north shore); lower panel: station 403 (midlake).

bacteria were counted per slide and the bacterial biovolume and biomass calculated as above. Cocci types were distinguished from rods and spirals.

Results

Pnano and Hnano were both common throughout the year in the surface water of Lake Ontario at the northshore (401) and midlake stations (403) and were typically present at densities of 1×10^3 to 5×10^3 cells·mL^{-1} (Fig. 1). Although Pnano was usually numerically dominant, there were times (mid-May for both stations and mid-August for 403) when Hnano was more abundant. These times followed peaks of Pnano. A single large peak of Pnano (1.6×10^4 cells·mL^{-1}) occurred at the end of June at 401 and lasted until mid-July. The June peak at 403 was greater than the one at 401 (2.3×10^4 cells·mL^{-1}) but declined earlier than at 401. A second peak occurred at the end of August at 403 but not at 401. On average, Hnano was more abundant at the deep station (0.6×10^3 to 8.0×10^3 cells·mL^{-1}) than at 401 (0.6×10^3 to 4.5×10^3 cells·mL^{-1}). The southshore station (405, not shown in Fig. 1) exhibited a seasonal pattern similar to that of 401 from June, when sampling began, onward. Peak abundance of Pnano occurred at the end of June (1.8×10^4 cells·mL^{-1}).

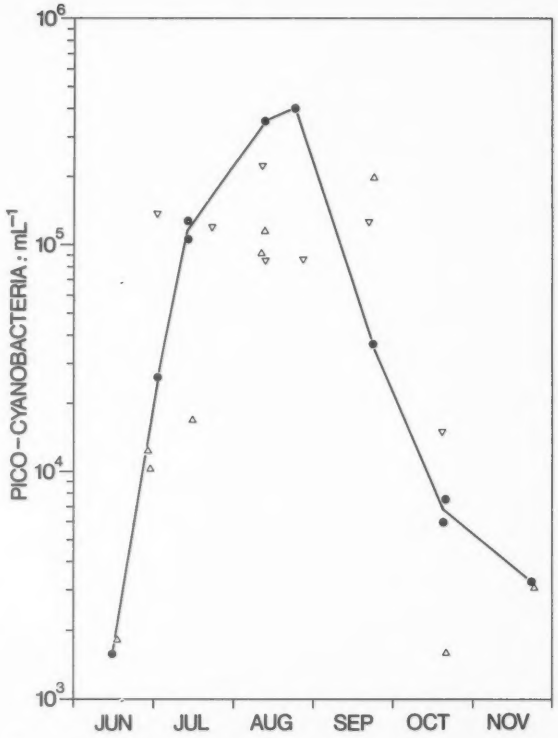

FIG. 2. Abundance of phototrophic picoplankton at stations 403 (●), 401 (△) and 405 (▽) at 5 m in Lake Ontario during 1982. A solid line is drawn through the 403 data set.

Ppico an Hpico in Lake Ontario were typically two to three orders of magnitude more abundant than the nanoplankton. The Ppico, predominantly chroococcoid cyanobacteria, showed the greatest seasonal change of abundance of all microorganisms <20 μm in size (Fig. 2) spanning four orders of magnitude (10^2 to 10^5 cells·mL^{-1}). Seasonal changes in their abundance during 1982 have been previously described (Caron et al. 1985). At all stations, Ppico increased exponentially from June through August, reaching an apparent "stationary phase" in late August which persisted longer at the inshore stations than at the midlake station. The highest concentrations were found in 401. Ppico decreased in a nearly exponential fashion during September and October at all three stations.

Hpico (heterotrophic and perhaps chemolithotrophic bacteria) followed a similar seasonal pattern to that observed for Ppico (Fig. 3). Hpico abundance began to increase in June and reached maximum abundance in July, August, and September at 405, 403, and 401, respectively. However, unlike the Ppico the seasonal change in bacterial density was less that one order of magnitude (1.0×10^6 to 6.4×10^6). Bacterial abundance was highly correlated with water temperature over the season ($r = 0.81$, $P < 0.001$), as has previously been noted for chroococcoid cyanobacteria in Lake Ontario (Caron et al. 1985). Bacterial abundance was also correlated with the abundance of chroococcoid cyanobacteria ($r = 0.70$, $P < 0.001$).

We observed two peaks in the biomass of microorganisms <20 μm in size at 5 m in Lake Ontario (Fig. 4). This depth is representative of the mid-euphotic zone and was typically the

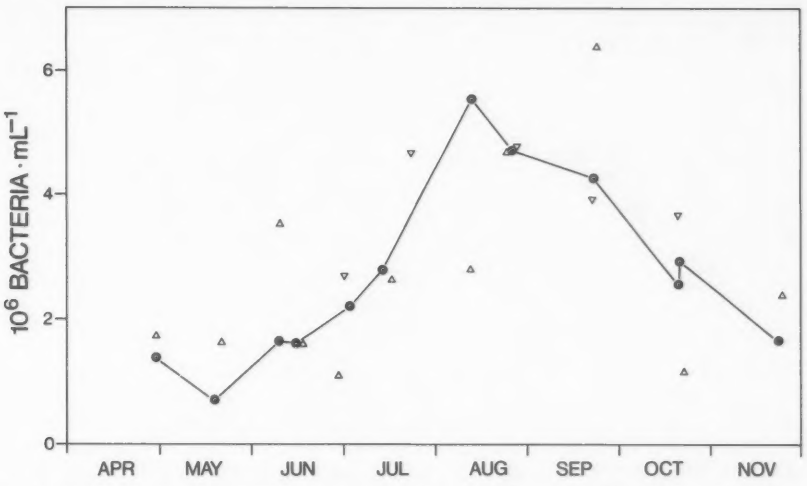

FIG. 3. Abundance (5 m) of bacteria at stations 401 (△), 403 (●) and 405 (▽). A solid line is drawn through the 403 data set.

depth of maximum abundance of microorganisms $< 20\ \mu m$ in size during stratification. The biomass of the $< 20\ \mu m$ group was highest at all three stations when Pnano biomass peaked at the end of June ($1.44\ g \cdot m^{-3}$ at 403 and $1.01\ g \cdot m^{-3}$ at 401). During this time, Ppico were only abundant at 405 (Fig. 2 and 3). The second biomass peak occurred in late August and was principally the result of the development of the picocyanobacteria populations and to a lesser extent the bacterial populations. At this time the relative contribution of the Pnano and Hnano biomass to the total biomass $< 20\ \mu m$ was reduced, especially at 401 and 403.

Although the mean cell volume of the picoplankton was small relative to the nanoplankton, picoplankton constituted a significant fraction of the total biomass of microorganisms $< 20\ \mu m$ in size because of their large densities. In fact, despite differences in numerical abundance in excess of three orders of magnitude between the four populations, biomass estimates rarely differed by more than one order of magnitude. A notable exception to this generalization was a low biomass of Ppico during periods of cold water. The large peak in Ppico biomass at the end of August at stations 401 and 403 constituted 49 and 39% of the total biomass $< 20\ \mu m$, respectively, and approximately 68% of the phototrophic biomass $< 20\ \mu m$ at both these stations. Hpico constituted a significant fraction of the total biomass $< 20\ \mu m$ throughout the study, ranging from 7% during the peak in Pnano biomass to 52% in spring, late summer, and fall (Fig. 4). Hpico biomass reached a maximum in August at stations 403 and 405 and in September at station 401.

The depth distribution of Pnano, Hnano, Ppico, and Hpico abundance is shown in Fig. 5, 6, and 7 in relation to the 8°C isotherm used to denote the metalimnion. The microbial populations, both phototrophic and heterotrophic, showed only minor differences in abundance with depth during isothermal conditions. During stratification, all populations showed substantial increases in abundance in the euphotic zone, but abundance below the thermocline remained relatively unchanged. A subsurface peak of abundance of the populations was observed in the epilimnion during this period. Ppico showed the most significant decline in numbers with depth, particularly in late August (Fig. 6). In contrast, Pnano was relatively abundant below the thermocline on all sampling dates (Fig. 5).

The depth distribution of microbial biomass $< 20\ \mu m$ on three dates during the summer of 1982 at stations 403 (Fig. 8) and 401 (Fig. 9) reflected the changes in population abundance described above. A subsurface biomass maximum was particularly apparent at both stations on August 12. Although phototrophs constituted a large fraction of the total biomass above the thermocline, heterotrophic biomass was more important below the thermocline, primarily due to the large biomass of bacteria. Nevertheless, Pnano biomass was still significant in deep water. Ppico biomass was relatively unimportant below the thermocline, particularly at 403 (Fig. 8).

Although we were more interested in numerical abundance and total biomass than a detailed species composition, identifications of specific subpopulations were made when possible. The Pnano was composed of green algae, diatoms, and cryptomonads. Red autofluorescent nonflagellated cells up to $5\ \mu m$ in size formed the large peak at the end of June and the beginning of July at 401, 405, and 403, respectively, but it was not possible to distinguish whether these were tiny centric diatoms or coccoid green algae, as both groups fluoresce an intense red. These cells were also common below the thermocline at 403 and together with *Scenedesmus bijuga*(2) and *Ankistrodesmus falcatus* formed the main photosynthetic forms below 50 m. Cryptomonads (*Rhodomonas minuta*, *Cryptomomas* sp.) were present on all sampling dates but reached maximum abundance in late summer and early fall. The Ppico were primarily of the chroococcoid *Synechococcus* type (Leppard et al. 1987) previously described in marine systems. At 401 a small filamentous blue-green ($3 \times 1.5\ \mu m$ rod), *Oscillatoria* sp., was usually found below the thermocline in summer and fall. This species reached a maximum concentration on 12 August, contributing to the large biomass peak at 10 m ($2.9 \times 10^4 \cdot mL^{-1}$) in the metalimnion (Fig. 9). Filamentous cyanobacteria were rare at 403. The Hnano was composed of flagellated Protozoa, both monoflagellated and biflagellated forms of the genera *Bodo* and *Monas*, between 3 and $10\ \mu m$ and rarely $> 10\ \mu m$. Choanoflagellates were also present at all stations. Heterotrophic *Gymnodinium* spp. were rare at the

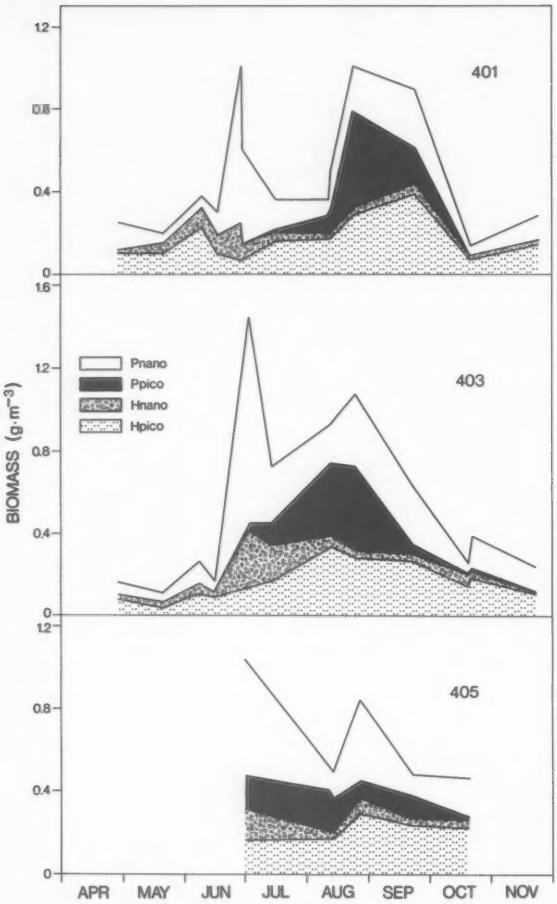

FIG. 4. Distribution of phototrophic an heterotrophic picoplankton and nanoplankton wet weight biomass at 5 m in Lake Ontario during 1982. The upper line represents the total biomass < 20 μm.

inshore stations and at 403 were only observed below the thermocline. Heterotrophic flagellates far outweighed the importance of ciliates in the Hnano < 20 μm in size.

Discussion

Maximum Ppico and Pnano biomass in Lake Ontario occurred from late June to late August and was minimal in spring and fall. However, total algal biomass estimated using the inverted microscopical technique on samples taken simultaneously with our samples showed maxima in the spring at 401 during development of the thermal bar and in early June at station 403 (Gray 1987). Therefore, it appears that algae in the picoplankton and nanoplankton size classes dominate the phytoplankton of the lake during periods of relatively low total algal biomass. This finding is consistent with predictions that the nanoplankton component of algal biomass decreases with increasing trophic status of lakes (Pavoni 1963; Gliwicz 1967; Watson and Kalff 1981).

The first detailed phytoplankton study of Lake Ontario made note of the presence of colorless chrysomonads, particularly during the summer and to a lesser extent in the fall, but no quantitative data on their abundance were provided (Munawar and Nauwerck 1971). In general, ecological studies of freshwater systems have neglected these microorganisms. Hnano constituted a significant portion of the total nanoplankton in Lake Ontario (Fig. 1). The concentrations of Hnano were similar to concentrations found in marine plankton (Caron et al. 1982; Davis and Sieburth 1982; Sherr et al. 1984; Davis et al. 1985), resulting in similar ratios of Pnano to Hnano (usually 3–2:1). Significant Hnano biomass is not unique to Lake Ontario and has been observed in other lakes (F. R. Pick unpubl data). Because heterotrophic forms are difficult to separate from chlorophyll-containing cells when Lugol's-stained samples are counted, the above findings suggest that as much as half (and occasionally all) of the nanoplankton enumerated by inverted microscope techniques can be heterotrophic and thus not photosynthetic phytoplankton.

Pnano and Hnano populations in the euphotic zone were weakly correlated ($r = 0.44$, $P < 0.01$) in Lake Ontario. This correlation has also been observed in the marine plankton (Davis et al. 1985). However, a more typical pattern during this study was a peak in Pnano followed by a peak in Hnano (Fig. 1). Hnano may be involved in the decrease in the abundance of Pnano either by preying directly on Pnano (Boraas 1983) or by accelerating the decomposition of dead Pnano cells, as has been demonstrated during the decline of a *Peridinium* bloom in Lake Kinneret (Sherr et al. 1982).

Recent investigations of marine pelagic communities have indicated that Hnano may be the primary consumers of bacteria and chroococcoid cyanobacteria (Azam et al. 1983). Hnano density has been correlated with the density of Hpico in the marine pelagic environment (Sherr et al. 1984; Davis et al. 1985), but often the two populations are temporally offset because of the time needed for predators (Hnano) to respond to increases in prey (Hpico) (Fenchel 1982; Davis et al. 1985). Such a relationship was not obvious in Lake Ontario, possibly because our sampling was not frequent enough. However, on a vertical scale, changes in Hnano paralleled depth changes in the rest of the microbial community. Microscopical observations also confirmed the importance of Hnano as consumers of picoplankton. For example, 15% of Hnano enumerated in late summer samples from the euphotic zone contained autofluorescent cyanobacteria in posterior food vacuoles (Caron et al. 1985). We therefore conclude that Hnano in Lake Ontario probably play as significant a role in this freshwater environment as consumers of picoplankton, as has been suggested for these microorganisms in marine systems.

Several workers have noted a relationship between bacterial and algal abundance over a range of lakes of different trophy (Wetzel 1975). The seasonal and vertical distribution of Hpico in Lake Ontario (Fig. 3 and 7) indicates that their abundance was associated with the activity of algae < 20 μm in size rather than being correlated with algae > 20 μm. Hpico abundance peaked during late summer and early autumn when Pnano and especially Ppico dominated the total algal biomass. Relatively low Hpico abundance occurred in the spring when algae > 20 μm dominated the total algal biomass (Gray 1987). However, it is difficult to attribute changes in Hpico abundance solely to changes in biological factors, since their abundance was highly correlated with temperature. This temperature dependence was more significant than that found by Rao et al. (1979) at an inshore Lake Ontario station and was as significant as the relationship found between temperature and the abundance of

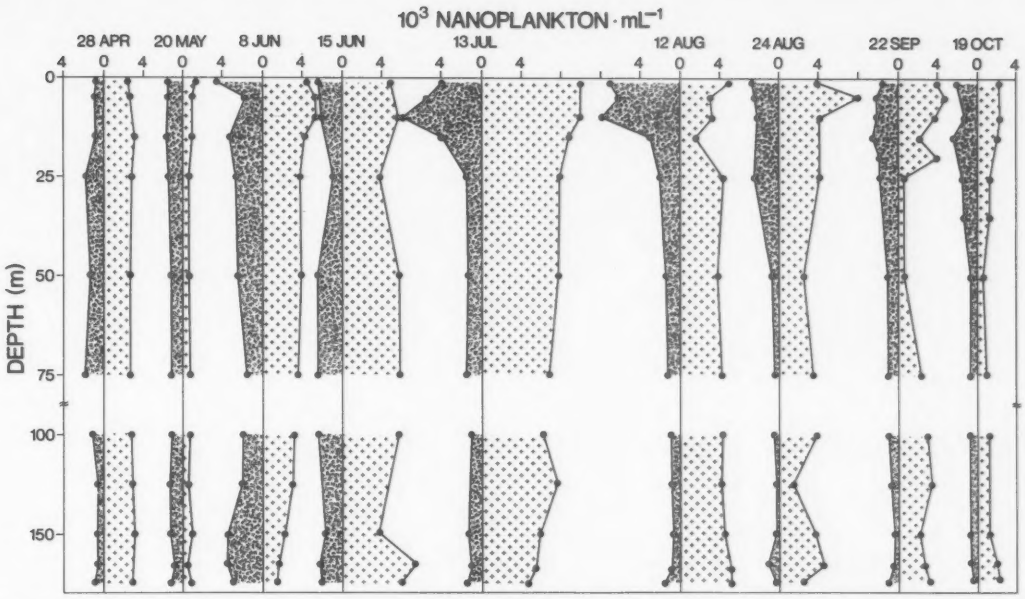

FIG. 5. Depth profiles of the abundance of phototrophic and heterotrophic nanoplankton at station 403 in Lake Ontario during 1982. Phototrophic nanoplankton are on the right and heterotrophic on the left of each panel representing a sampling date.

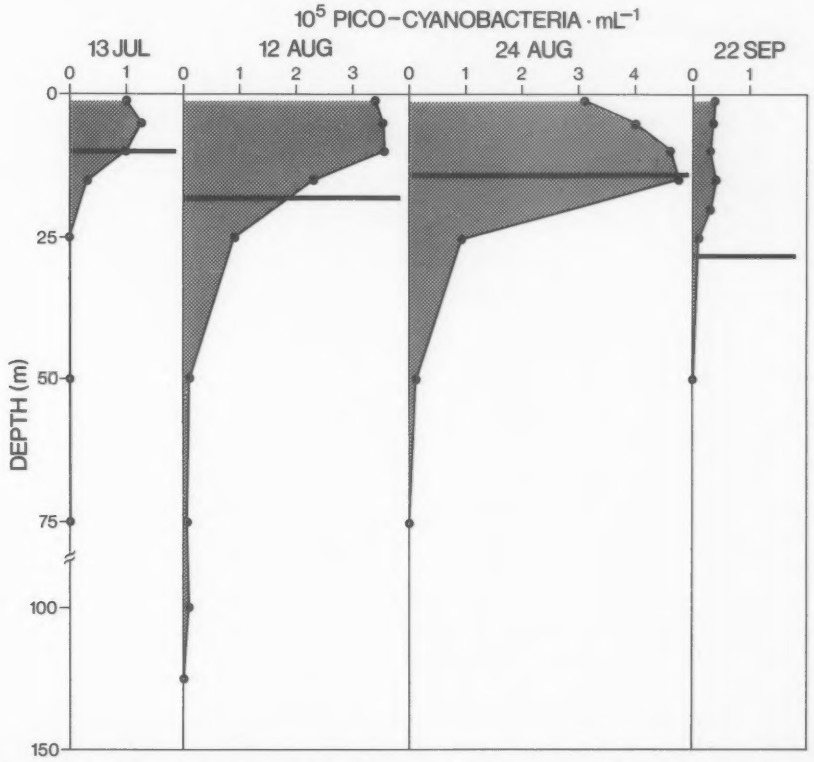

FIG. 6. Depth profiles of abundance of phototrophic picoplankton at station 403 in Lake Ontario during 1982. Horizontal lines represent the 8°C isotherm.

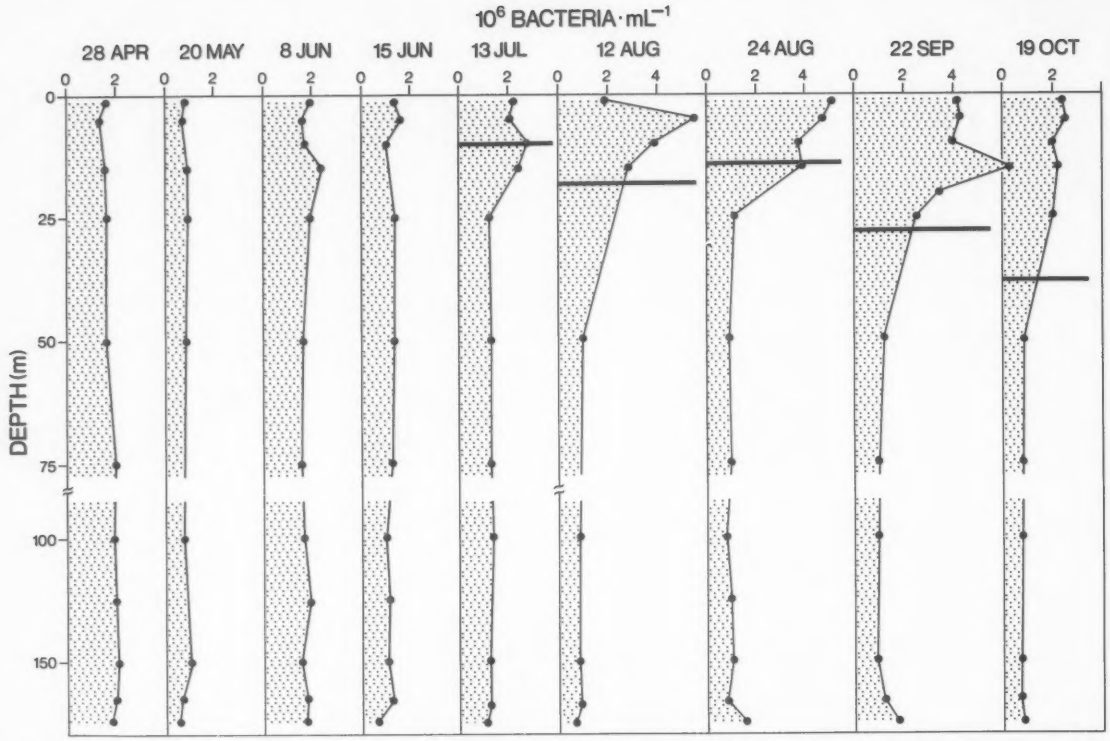

FIG. 7. Depth profiles of abundance of heterotrophic picoplankton at station 403 in Lake Ontario during 1982. Horizontal lines represent the 8°C isotherm.

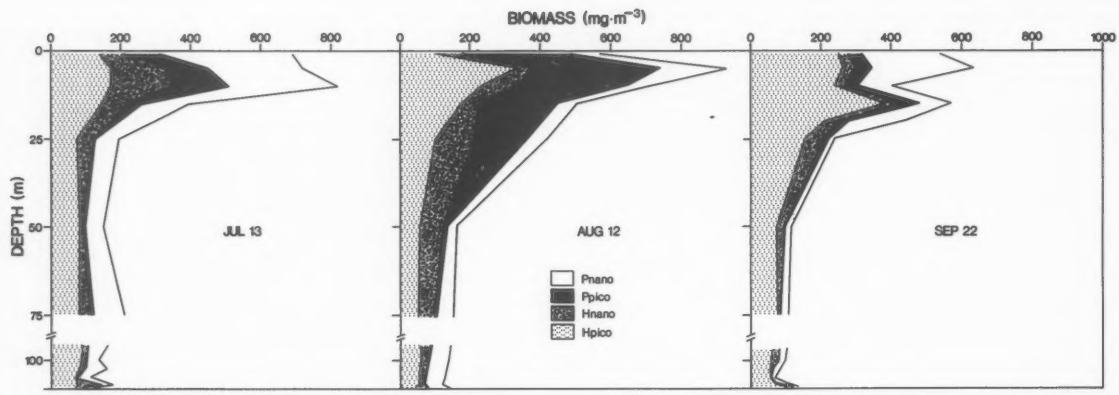

FIG. 8. Representative depth profiles of phototrophic and heterotrophic picoplankton and nanoplankton wet weight biomass at station 403 in Lake Ontario during 1982.

chroococcoid cyanobacteria in Lake Ontario (Caron et al. 1985). Hpico was not concentrated in the aphotic zone as is often depicted in general texts (Round 1980). Bacterial abundance in the epilimnion was always greater than or equal to abundance in the hypolimnion, and on only two dates (24 August and 19 September) was an increase in abundance observed in the samples 2 m above the sediments (Fig. 7).

Our work clearly demonstrates that picoplankton, consisting largely of phototrophic and heterotrophic prokaryotes, constituted an important fraction of the total biomass of microorganisms $< 20\ \mu m$ (74% in mid-August at 403, Fig. 4). This is contrary to conclusions of Sprules et al. (1983) who found a "trough" in particle spectra of lakes in the 0–2 μm region, indicating that "bacteria and small algae contribute comparatively minor amounts of biomass." If a summer epilimnetic average for total biomass of picoplankton (470 mg wet weight·m^{-3}) in Lake Ontario is placed in any one of their spectra, the "trough" at 0–2 μm disappears.

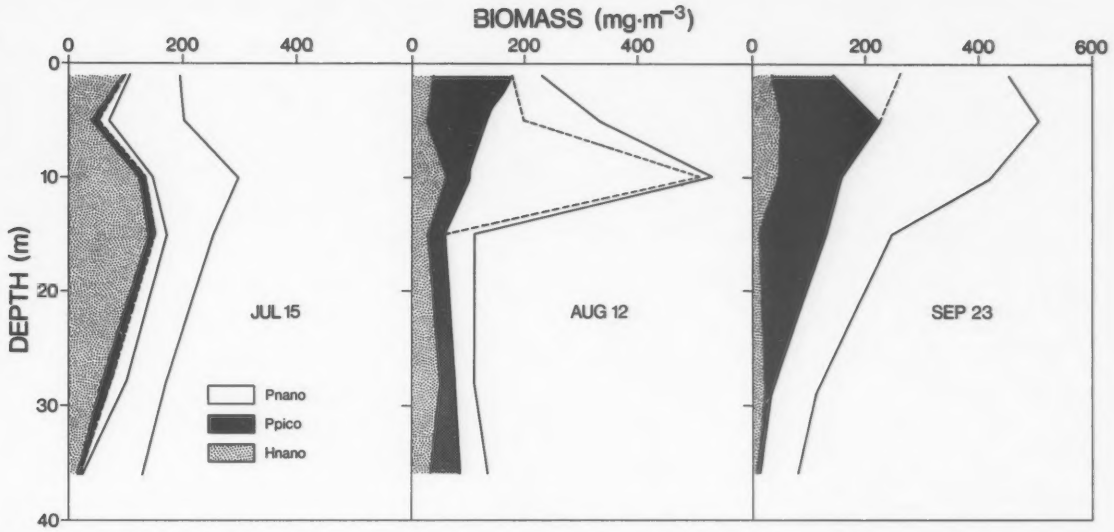

FIG. 9. Representative depth profiles of phototrophic picoplankton and nanoplankton and heterotrophic nanoplankton wet weight biomass at station 401 in Lake Ontario during 1982. Broken line divides filamentous cyanobacteria (left) from the rest of the phototrophic nanoplankton (right).

Munawar et al. (1974) provided size-fractionated algal biomass for Lake Ontario and showed that the < 20 μm fraction accounted for as much as 40% of the total algal biomass at a midlake station during 1972–73. Nanoplankton (defined in that study as microorganisms < 64 μm) biomass peaked at a nearshore station at the end of June 1972 (as it did in our study) and a single peak occurred at the midlake station in September (no sampling was conducted in August). While these seasonal trends are consistent with the results of the present study, we have observed that the abundance of microorganisms 2–20 μm in size as estimated by epifluorescence microscopy at times exceeded the total biomass estimates obtained by the Utermöhl technique (Gray 1987) because of the underestimation of cells < 5 μm in size. This underestimation was particularly striking in late August at all stations when the epifluorescence biomass estimates were three times higher than the Utermöhl estimates of Gray (1987). In addition we have observed that picoplankton-sized phototrophs, which have been previously overlooked by the Utermöhl technique, constituted an important fraction of the photosynthetic biomass < 20 μm. We conclude that, for a more accurate estimation of algal biomass, epifluorescence techniques should be incorporated into freshwater phytoplankton field studies. While the Utermöhl technique is still superior for the enumeration of algae > 20 μm such as diatoms (F. R. Pick unpubl. data), it is inappropriate for differentiating Hnano and Pnano. The combined use of both techniques is therefore recommended for future investigations.

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Characterization of Cyanobacterial Picoplankton in Lake Ontario by Transmission Electron Microscopy

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Many chroococcoid cyanobacteria from Lake Ontario, characterized by epifluorescence in concert with transmission electron microscopy, had a Type I ultrastructure, the major type in oceanic waters. Such cells had a multilayered cell envelope and their polyhedral bodies were interspersed with the central nuclear material. All thylakoids were peripheral and were arranged concentrically, with no intrusion into the nuclear region. Related chroococcoid types were also seen but these were much less abundant. The most numerous cell type in all water samples was a small, Gram-negative, rodlike bacterium. Many of these rods were sufficiently small to pass a filter of 0.45-μm pore size but none had a diameter less than 0.2 μm. Attempts to isolate and describe the cyanobacterial picoplankton presented some unusual difficulties having a potential to mislead limnological analyses. These are described and, to some extent, they are resolved here.

Un grand nombre des cyanobactéries chroococcales peuplant le lac Ontario, caractérisées par une épifluorescence de concert avec une observation au microscope électronique à transmission, possédaient une ultrastructure de type I omniprésent en milieu océanique. Ces cellules possédaient une paroi cellulaire à plusieurs couches et leurs corps polyhédriques étaient répandus dans la matière nucléaire centrale. Tous les thylakoïdes étaient en position périphérique et disposés concentriquement sans intrusion dans la région nucléaire. On a aussi observé des chroococcales apparentées, mais en nombre beaucoup plus petit. Une petite bactérie bacilliforme gram-négative constituait le type de cellules le plus abondant dans tous les échantillons d'eau. Un grand nombre de ces bacilles étaient suffisamment petits pour traverser un filtre à pores de 0,45μm, mais aucun n'avait un diamètre inférieur à 0,2μm. On a éprouvé certaines difficultés exceptionnelles au cours des essais d'isolation et de description des cyanobactéries picoplanctoniques. Ces difficultés, qui pourraient biaiser les analyses limnologiques, sont décrites et, dans une certaine mesure, résolues.

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For many years, microscopical investigations have been revealing that microbes of unusually small dimensions, both bacterial (Bae et al. 1972; Sieburth et al. 1978) and algal (Manton 1959; Johnson and Sieburth 1982), may be common in nature despite their rarity in laboratory cultures. This is true of some soils where up to 72% of microbial cells can have diameters less than 0.3 μm (Bae et al. 1972). This is also true of surface waters where the phenomenon is documented for estuaries (Johnson and Sieburth 1982) and oceanic waters of tropical (Waterbury et al. 1979; Johnson and Sieburth 1979; Li et al. 1983), temperate (Manton 1977; Johnson and Sieburth 1979, 1982), and arctic types (Johnson and Sieburth 1982). As a consequence of these findings, attention is now being focussed on the picoplankton of lakes (Sicko-Goad and Stoermer 1984; Caron et al. 1985). The application of transmission electron microscopy (TEM) to picoplankton studies and to the study of natural microbial populations in general continues to reveal the ubiquitousness of unusually small microbes (0.2–0.4 μm), including some as small as 0.1 μm in diameter (von Hofsten et al. 1971).

Physiological studies on lake community metabolism have shown that microbes with diameters approaching the lower limit for both prokaryotic and eukaryotic cells make a disproportionately great contribution to primary production (Munawar et al. 1978). These findings have been complemented by oceanographic investigations of the physiological importance of aquatic microbes in the smallest size category for cells, the picoplankton (0.2–2.0 μm). For example, Li et al. (1983) found that up to 90% of the phytoplankton biomass and up to 80% of the inorganic carbon dioxide fixation in one tropical oceanic water were found in a particle fraction which passed through a screen having a pore diameter of 1 μm.

This paper addresses itself to the characterization of lacustrine cyanobacterial picoplankton in Lake Ontario and to the

technical problems of fractionating lake water so as to obtain representative picoplankton populations, while minimizing any artifactual selective losses of cell types.

Methods

Water samples were taken from epilimnetic water of Lake Ontario at a midlake station (403, 43°35′52″N, 78°13′51″W) on 28 August 1984 during a period when microbial biomass is typically at a maximum (Pick and Caron 1987). Fresh and preserved samples (final 1% glutaraldehyde solution buffered with cacodylate) were examined by epifluorescence microscopy as outlined in Caron et al. (1985). Whole lake water and lake water filtered through 8-, 5-, and 1-μm Nuclepore polycarbonate membranes were enumerated for chroococcoid cyanobacteria, photosynthetic nanoplankton, and heterotrophic nanoplankton by autofluorescence. Bacteria were enumerated using the fluorescent stain DAPI (Porter and Feig 1980).

The initial stages of the preparation of microbiota for examination by TEM were done as follows: a freshwater sample was poured through an 8-μm membrane (see above) and fresh filtrate was mixed gently with a buffered aldehyde fixative (at the same temperature as the water sample) to give a final concentration of 3.4% glutaraldehyde and 0.08 mol/L cacodylate–HCl buffer at pH 7. The filtrate and the fixative were mixed in approximately equal portions to optimize the rate of fixative penetration. In the laboratory, all subsequent chemical preparation for TEM was carried out according to Burnison and Leppard (1983) with a second filtration step interposed as follows. The glutaraldehyde-fixed cells were collected on a 0.4-μm filter (Nuclepore N40 polycarbonate membrane) using an added filtration pressure of 70 kPa. While still moist, the filter's upper surface and its adhering microbiota were coated with a thin layer of warm (60°C) liquid agar (0.6% Agar Technical No. 3 from Oxoid); when the agar had gelled, a strip of the filter–microbe–agar continuum was processed chemically as a unit, starting at the secondary fixation stage. The counterstained sections of 50- to 70-nm thickness were observed and photographed with a Philips 300 TEM.

The overall preparatory scheme above was derived by integrating a series of water fractionation schemes (involving centrifugation and/or cascade filtration) with several chemical fixation procedures. Preliminary testing conducted on samples collected in 1982 from Lake Ontario gave insight into some anomalous behaviour of the chroococcoid cyanobacteria with regard to fractionation schemes used previously for concentrating them.

Results and Discussion

Concentrations of microbes, estimated by epifluorescence counts, were of the same order of magnitude (Table 1) as in previous years for August (Caron et al. 1985; Pick and Caron 1987). Chroococcoid cyanobacteria were of the phycoerythrin-containing type that autofluoresces yellow–orange in epifluorescence microscopy. Both fresh and preserved samples gave similar estimates for these populations (1.75×10^5/mL). One hundred percent of these cells passed the 8-μm filter whereas only 87% passed the 5-μm filter. For this reason, the 8-μm filter was used in TEM preparations. In other lakes where chroococcoid cyanobacteria are as abundant and of similar size (0.7–1.2 μm in diameter), less than 50% may pass a 5-μm filter,

TABLE 1. Microbial populations estimated by epifluorescence microscopy in Lake Ontario, 28 August 1984.

	Whole lake water (no./mL)	8 μm (as a % of whole lake water)	5 μm (as a % of whole lake water)	1 μm (as a % of whole lake water)
Bacteria	5.23×10^6	100	100	89
Chroococcoid cyanobacteria	1.75×10^5	100	87	23
Photosynthetic nanoplankton	3.23×10^3	90	80	0.9
Heterotrophic nanoplankton	1.52×10^3	96	83	4

suggesting that colony formation or aggregation may be extremely variable (F. R. Pick, unpubl. results).

The most common chroococcoid cyanobacteria found, using TEM criteria, were spherical to oval cells of Type I ultrastructure as characterized by Johnson and Sieburth (1979) and illustrated by the dividing cell of Fig. 1. This cell type, previously found to be ubiquitous in oceanic surface waters (Johnson and Sieburth 1979), has the following general characteristics in epilimnetic Lake Ontario water.

(1) It has a multilayered cell envelope which sometimes displays an outermost extra layer of electron-opaque material, after counterstaining. This extra layer can be highly structured in the manner described earlier by Kursar et al. (1981).

(2) It has a peripheral thylakoid, or peripheral thylakoids arranged concentrically, with no intrusion into the nuclear region. The thylakoids number as many as three but not all of them encircle completely the cytoplasm.

(3) The thylakoids have a membrane structure which is difficult to resolve as one sees by comparing the thylakoid ultrastructure of the cyanobacterium in Fig. 2 with that of the large eukaryotic alga also present in Fig. 2. The difficulty resides partly in the extreme curvature of the thylakoids relative to section thickness (Fig. 1 and 2) and partly in the extreme compression of thylakoid structure as revealed by the high magnification micrograph of Fig. 3.

(4) In cells containing either two or three peripheral thylakoids, the thylakoids are widely interspaced by densely packed, electron-opaque cytoplasmic material (Fig. 1).

(5) The central nuclear material is interspersed with several polyhedral bodies of varying electron density relative to the cytoplasm (Fig. 1).

(6) The diameter is more variable than the documented range for Type I cells in oceanic waters (0.8–1.0 μm). Discounting cells undergoing division, the range of diameters for Lake Ontario cells extended downwards into the ranges previously established for Type II (0.7–0.9 μm, see Fig. 5) and Type III cells (0.4–0.5 μm, see Fig. 6) as documented by Johnson and Sieburth (1979).

It is possible to split the lacustrine Type I cells arbitrarily into several subtypes. This can be done with respect to growth habit (e.g. the unicell of Fig. 1 versus the four-celled colony of Fig. 4), the number of thylakoids, and the structure of the outermost wall layer (e.g. the fibrous layer revealed by Fig. 5 versus the layer of repeating subunits shown in Fig. 6). To establish a subtype classification scheme and to ascertain the relative proportion of each subtype is, however, an endeavor beyond the scope of this initial study. The variability of Type I cells was

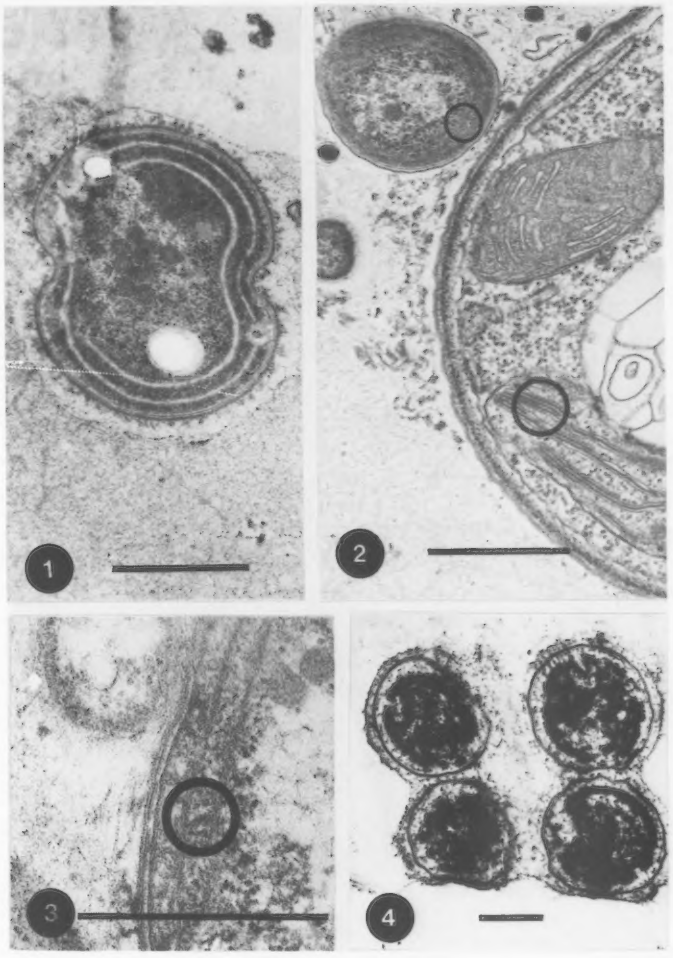

FIG. 1. Dividing cell of a Type I chroococcoid cyanobacterium, with two thylakoids and an extra layer of wall structure projecting into the external milieu. FIG. 2. Effect of a tightly imposed curvature on the resolution of thylakoids. The small size of a chroococcoid cell, relative to section thickness, means that most views of its thylakoids will be equivalent to a glancing section through the thylakoids of a large cell. Compare the image of the thylakoids in the chroococcoid cell (small circle) with the image presented by the large eukaryotic cell (large circle). FIG. 3. Median longisection view through a relatively large chroococcoid cell at high magnification. In views such as this, thylakoid structure is more evident, as shown within the large circle. FIG. 4. Colony of four chroococcoid cells encased in a sheath. Bars = 0.5 μm.

great enough that cells could be found with characteristics which blurred the distinctions between the accepted types as they were originally documented in the marine literature. Figure 7 shows a cell whose size is in the Type I range and whose outer wall layer resembles that of many Type I cells. However, its thylakoid arrangement is atypical for Types I, II, and III as described by Johnson and Sieburth (1979), and the spatial relationship between its thylakoid and its nuclear region is more like Type III than Type I. This cell (Fig. 7) has characteristics indicating a poor condition at the time of fixation. Had such a cell been seen as a rarity in a laboratory culture, it would have been ignored. However, such cells occur in varying abundance in natural populations (G. G. Leppard, unpubl. results) and they may contribute to the physiological activities measured by limnologists; for this latter reason, more knowledge of their impact on water quality is needed now.

The unicellular cyanobacteria were associated with much greater numbers of small bacteria having a Gram-negative wall structure. Many of these bacteria were much smaller than 0.4 μm in diameter, with some well-preserved specimens showing least diameters (as measured in median cross-sections from the outermost tripartite layer of the cell envelope) approaching

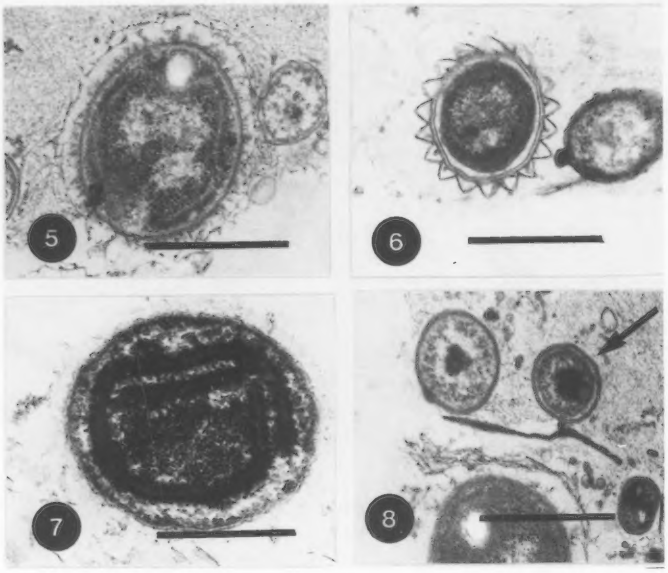

FIG. 5. Type I cell in the Type II size range. Compare with Fig. 1 and 6. FIG. 6. Type I cell in the Type III size range. Note the geometrical array of structural units representing the outermost wall layer. Compare with Fig. 1 and 5. FIG. 7. Cyanobacterium with intermediate features. FIG. 8. Unusually small nonphotosynthetic bacterium common to Lake Ontario picoplankton. Bars = 0.5 μm.

0.25 μm (Fig. 8). These probably would not be enumerated accurately using epifluorescence techniques. It is possible that small bacteria which did not pass the 0.4-μm filter were part of loose aggregates. Cross-connecting fibrils of the type described in Burnison and Leppard (1983) could be seen rarely, but the use of the fibrillar agar overlay precluded an analysis of fibril-mediated aggregation.

Among the other cell types seen in the 0.4–8 μm fraction were unicellular eukaryotic algae and some protozoa, but these were not commonly encountered. They were several orders of magnitude less abundant (Table 1) than the Gram-negative rods and the cyanobacteria. While these latter cells were studied intensively only at the sample site and date given above, they were seen in all Lake Ontario water samples taken for preliminary investigations in 1982. At this time, experiments on the fractionation of lake water were carried out to devise an optimal approach to concentrate picoplankton for TEM analyses.

Standard approaches to concentrating the Type I cells led to great losses of cells, including selective losses of cell types as judged by TEM monitoring (Burnison and Leppard 1983). Some particular problems were identified and these are summarized as follows: (1) the many fluid changes and washes employed in the cytological processing required for TEM were undesirably effective in detaching Type I cells from fine filters used to trap natural microbial populations, thus leading to disproportionate losses of Type I cells; (2) low-speed centrifugation (up to 1400 × *g*) was ineffective in concentrating chroococcoid cells; (3) the distribution of chroococcoid cells on the surface of filters with pore sizes near 0.5 μm was always patchy to an extreme degree, even on the filter of choice (Nuclepore N40 polycarbonate membrane), thus suggesting that these cells approach a filter surface as aggregates.

The first problem was solved using an agar overlay to glue all particles (0.4–8 μm) onto the filter surface at an early stage of cytological processing and the second was solved by abandoning the use of low-speed centrifugation. The patchiness problem was solved by taking an inordinately great number of sections to obtain the required number of images for a morphological study. This third problem suggested that unicellular picoplankton can aggregate (or are aggregated by physical effects during concentration by cascade filtration). Through the use of an 8-μm screen in conjunction with epifluorescence microscopy, we determined that any aggregates present have a major diameter less than 8 μm. The largest colonial chroococcoid seen (the four-celled colony of Fig. 4) had a major diameter of 3 μm, so such colonies would not be excluded at the screening stage.

Once we could demonstrate that our TEM analyses included an entire population of chroococcoid cyanobacteria in a water sample, an observation was made which has a bearing on future attempts to concentrate and/or isolate other members of the picoplankton. The Gram-negative nonphotosynthetic bacteria with a diameter less than the pore diameter of the trapping filter were more numerous on the filter surface than were the Type I cells. Some of these bacteria had a diameter 40% smaller than that of the filter pores. How were they trapped and what proportion of such small bacteria do they represent? Some of the small bacteria could be found trapped deep within the filter pore structure, an observation which complements that of Burnison and Leppard (1983) who used a filter of 0.45-μm pore size to make separations. It is clear that a straightforward consideration

of cell size versus pore size is not sufficient as a sole basis for the design of cascade filtration schemes employed to isolate sedimenting units which grade into the colloidal size range.

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Zooplankton Seasonal Succession in Lake Ontario at Northshore, Midlake, and Southshore Stations in 1982, and a Comparison with 1970

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The seasonal pattern of zooplankton succession in Lake Ontario was similar at three stations along a north–south transect, with differences attributable to physical factors. Because of warming within the thermal bar zone, the spring succession at the northshore station was early relative to the midlake station, but after stratification the northshore station lagged behind due to frequent upwelling events. Thermal bar formation along the south shore was followed by downwelling throughout the summer, giving a deeper epilimnion. These events may have contributed to not only the greater biomass at this location, but also succession which preceded that at the other stations during summer and fall. The species composition and the timing of the summer succession were very similar to those reported for 1970. Lake Ontario zooplankton did not change markedly in response to changes in nutrient loading and salmonid predators during the 1970's.

Le régime saisonnier de succession du zooplancton dans le lac Ontario était semblable à trois stations le long d'un transect orienté nord-sud, les différences étant attribuables à des facteurs physiques. En raison du réchauffement à l'intérieur de la zone de stratification thermique, la succession printanière à la station de la rive nord était précoce par rapport au milieu du lac mais, après stratification, la station de la rive nord était en retard en raison de remontées fréquentes d'eau. La formation d'une strate thermique le long de la rive sud a été suivie d'une descente d'eau pendant tout l'été faisant descendre ainsi l'épilimnion. Ces phénomènes pourraient avoir contribué non seulement à accroître la biomasse à cet endroit, mais également à la succession qui a précédé celle qui s'est produite aux autres stations en été et en automne. La composition des espèces et le moment de la succession estivale étaient très semblables à ceux signalés pour 1970. Le zooplancton du lac Ontario n'a pas changé de façon marquée suite aux changements dans l'apport de substances nutritives et dans les prédateurs de salmonidés pendant les années 70.

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The last major survey of the zooplankton of Lake Ontario was during the 1972 International Field Year for the Great Lakes (IFYGL). Zooplankton samples were taken at several locations, with special emphasis on nearshore waters (Czaika 1974, 1978). Previous to IFYGL, extensive collections were made in 1967 and 1968 (Patalas 1969) and in 1970 (Watson and Carpenter 1974). Earlier collections are much less extensive, but did allow McNaught and Buzzard (1973) to comment on long-term changes. They concluded that the zooplankton of Lake Ontario in 1972, dominated by *Bosmina longirostris* and *Diacyclops thomasi*, had replaced an earlier fauna dominated by *Diaptomus* spp. and *Daphnia* spp. Similar changes have been documented in Lake Michigan and attributed to increases in planktivorous alewives (*Alosa pseudoharengus*) following the decline of piscivorous salmonids (Wells 1970). In contrast, Patalas (1972) attributed the zooplankton fauna of Lake Ontario, relative to the calanoid-dominated fauna of the upper lakes, to eutrophication.

Physical factors certainly play a major role in shaping the zooplankton community of Lake Ontario. Patalas (1969) emphasized the importance of the heat content of the epilimnion. Using the 1972 IFYGL data, Watson (1988) found an exponential relationship between zooplankton biomass and water temperature in the top 25 m. Both Patalas (1969) and Watson (1988) mentioned the importance of upwelling events in altering zooplankton communities.

Since 1972, Lake Ontario has continued to change; spring total phosphorus has been reduced by about 50% (without a commensurate decrease in chlorophyll, Stevens and Neilson 1987), and salmonid fishes have greatly increased under an

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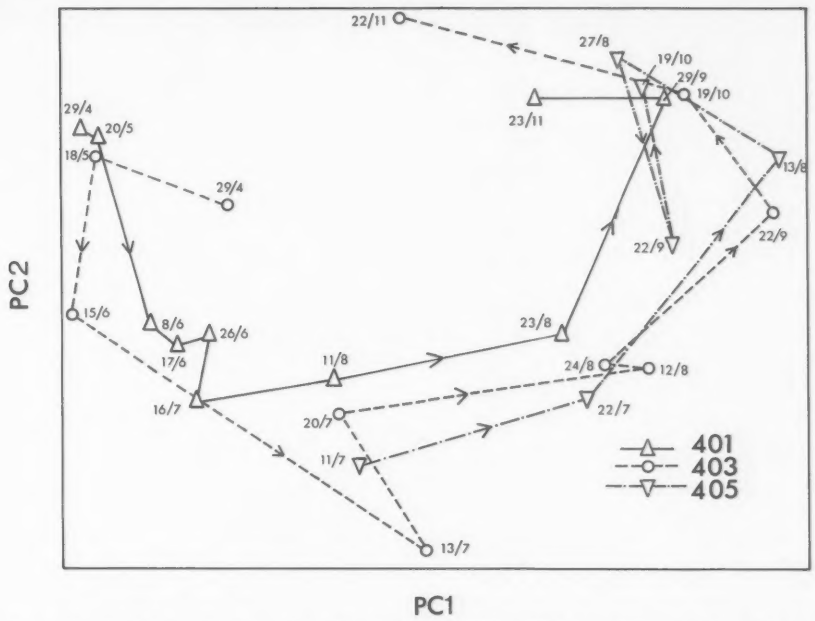

FIG. 1. Seasonal succession for stations 401 (northshore), 403 (midlake), and 405 (southshore) during 1982 displayed as trajectories on a principal components ordination. The relationship between the principal components and zooplankton species is given in Table 1.

aggressive stocking program (Great Lakes Fishery Commission 1983). Similar stocking in Lake Michigan has produced reductions in planktivore biomass and simultaneous alterations in the plankton (Scavia et al. 1986). These alterations include increases in large *Daphnia* and in transparency.

Planktivore biomass in Lake Ontario has varied greatly; the late 1960's and early 1970's were a period of high alewife biomass accompanied by nuisance die-offs. The mid-1970's had much lower alewife biomass, possibly due to increased numbers of salmonid fishes but especially following a major episode of winter mortality in 1976. Numbers remained relatively low throughout 1982 according to data on impingement of alewives at Pickering Nuclear Generating Station (R. Hester, Ontario Hydro, pers. comm.). Assessment trawling by the U.S. Fish and Wildlife Service and New York Department of Environmental Conservation indicates increasing numbers of alewives from 1978 to 1982 (O'Gorman and Schneider 1986), but earlier estimates are not available. Declines in alewife condition and growth occur in peak years, suggesting that Lake Ontario planktivores strongly affect their resources. In the Kingston Basin, alewife numbers also increased in the early 1980's to levels similar to 1970 and 1972 (Christie et al. 1987). Therefore it is clear that the planktivore stocks have undergone major changes since 1970, although we are not certain whether 1982 stocks are significantly lower than 1970 stocks at our stations.

In this report, we demonstrate the role of the physical environment in shaping the zooplankton community of Lake Ontario by comparing seasonal changes in abundance and vertical distribution of zooplankton from northshore, midlake and southshore stations. We then compare our 1982 data with that collected in 1970 by Watson and Carpenter (1974).

Materials and Methods

Samples were collected during April through November 1982 from three stations. Stations 401 and 405 were located on the north and south side of the lake, respectively, at a depth of 38 m. Station 403 was a midlake station, at a depth of 178 m. Details of location, physics, and chemistry are published elsewhere (Lean et al. 1987; Simons and Schertzer 1987).

Vertical hauls were taken using an unmetered 0.56-m-diameter net constucted with 64-μm nylon mesh and a ratio of 3:1 between filter area and mouth area. It was hauled from 2 m above the bottom at a speed of 0.5 $m \cdot s^{-1}$. Similar methods were used by Watson and Carpenter (1974) to collect the 1970 data, but midlake hauls were from 50 m with a 0.4-m net. Some discrete-depth samples were taken with a Schindler–Palatas Plexiglas sampler (Schindler 1969) but more extensively as part of zooplankton grazing experiments using 10-L grazing chambers (Haney 1971). Grazing chamber contents were collected on 64-μm and then 30-μm screens. All samples were preserved in a sugar–formalin solution (Haney and Hall 1973).

Identifications were made using Brooks (1957), Czaika and Robertson (1968), Deevey and Deevey (1971), Edmondson (1959), Nauwerck (1978), and Torke (1974). Immature stages of *Diaptomus* spp. and Cyclopoida were not identified. They were used in biomass estimates, but not in the ordinations based on species composition. Some rotifers were identified only to genus, but were included in ordinations.

The average mass of important species was determined from measurements of length and published length–weight relationships (Dumont et al. 1975; Bottrell et al. 1976; Rosen 1981). For other taxa, we used average biomass values from Hawkins and Evans (1979) and Wilson and Roff (1973). Approximate

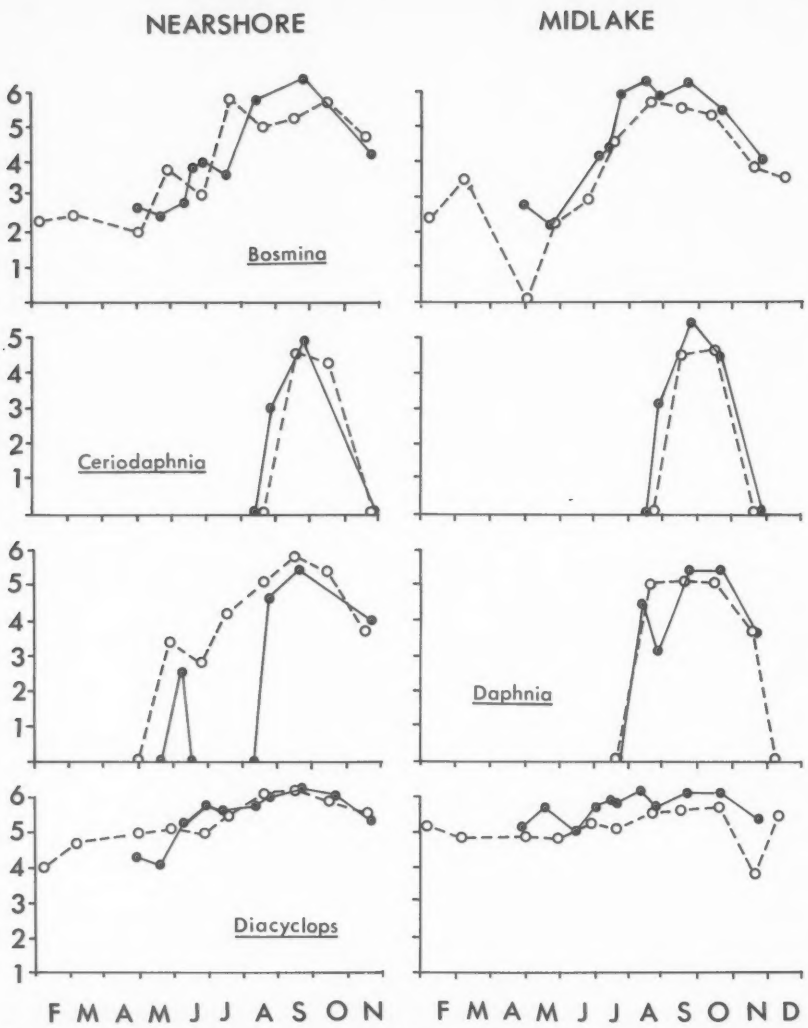

FIG. 2. Abundance of major crustacean zooplankton taken in net hauls during our study at stations 401 (nearshore) and 403 (midlake) and by Watson and Carpenter (1974) in 1970 from nearby stations. Abundance is expressed as $\log_{10}$ (number·m^{-2}) Broken lines, open circles — 1970; solid lines, solid circles — 1982.

biomass of zooplankton was calculated as the sum across species of the product of abundance and estimated average mass.

Principal components ordinations were used to summarize faunal data by combining correlated species into two derived "principal components" which express much of the total variation in common species (Gates et al. 1983; Pielou 1984). The principal component axes were extracted from the correlations among species after logarithmic transformation of abundances. Complete abundance data can be found in Fricker and Abbott (1985).

Results

Seasonal changes in the species composition of net hauls at three stations during 1982 are expressed as trajectories on principal components ordinations in Fig. 1. The first pricipal component (PC1) represents the abundance of the summer Cladocera *B. longirostris*, *Daphnia retrocurva*, and *Ceriodaphnia lacustris* (Table 1). It is also correlated with the summer rotifers *Keratella cochlearis*, *Polyarthra* sp., and *Trichocerca* sp. The second principal component (PC2) separates spring and fall samples from summer ones; its strongest correlations to species are negative, so diverse summer samples have low PC2 scores. Positive correlations with PC2 are with the few species abundant in early spring and late fall. The ordination represents about half of the variation present in the reduced data set; species that contribute little to the ordination include *Eubosmina longispina* and *Filinia* sp. (Table 1).

The three stations underwent similar seasonal cycles, but differed in their timing. Northshore station 401 is advanced relative to midlake station 403, as indicated by its higher PC1

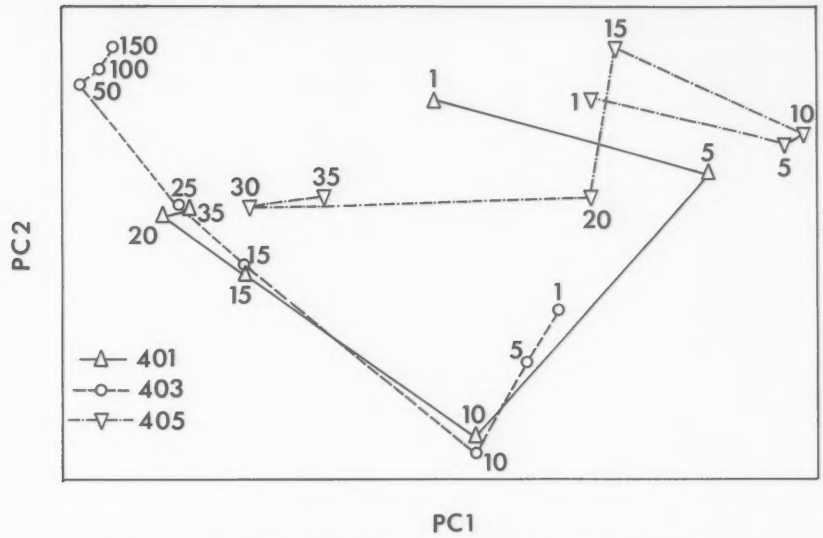

FIG. 3. Principal components ordination of the contents of grazing-chamber samples to illustrate depth profiles in late summer. Station 401 was sampled August 23, 1982, at 2235–0045, station 403 was sampled August 27, 1982, at 0350–0420, and station 405 was sampled August 27, 1982, at 0045–0215. Numbers on the ordination indicate sample depth (m).

score, during spring until mid-June. Station 403 passes 401 by July 13 and remains ahead on PC1 for the rest of the summer. Station 405, on the south side of the lake, was not sampled in spring. In mid-July it is similar to 403 but is ahead of 403 and 401 through August. Late September and October samples are similar for all three stations.

The seasonal succession we observed in 1982 is very similar to that seen by Watson and Carpenter (1974) in 1970 for comparable stations, especially midlake (Fig. 2). There do not appear to be major changes in the most important crustacean taxa. The strongest differences is the relatively late development and relatively lower numbers of *Daphnia* spp. at the northshore station in 1982. Although we had fewer samples from southshore station 405, a similar later development of *Daphnia* was seen in 1982 (not shown).

The differences among stations during 1982 are also evident in their midsummer depth profiles. Grazing-chamber collections were subjected to principal components ordination, and late August profiles are illustrated in Fig. 3. The composition of the principal components is similar to that shown in Table 1 and is therefore not presented. Deep samples from all stations are similar and have low PC1 scores. The 50- to 150-m depths from station 403 are particularly springlike in comparison with the seasonal ordination shown in Fig. 1. At stations 401 and 403, samples from 1, 5, and 10 m have high PC1 scores, while station 405 has high PC1 scores to 20 m. Samples from 15 m at stations 401 and 403 are similar to 30-m samples from station 405.

The vertical distribution of temperature and some of the most important zooplankton species emphasizes that the differences among the stations are related to the depth of the epilimnion (Fig. 4). Densities of zooplankton are similar across the lake, but warm temperatures and high densities extend much deeper on the south shore. However, it is also clear that the southshore fauna is not simply increased in proportion to epilimnion thickness; important rotifers are reduced relative to *Bosmina*. The thicker hypolimnion at station 405 also highlights the complimentary distributions of *D. thomasi* adults and copepodids.

TABLE 1. Correlation between derived principal components (eigenvectors) 1 and 2 of Fig. 1 and the original species variables. The third column contains the percent variance summarized for each variable by the two components. The last row contains the percent of total variance explained by each of the principal components.

Species	PC1	PC2	% variance
Bosmina longirostris	0.87	−0.12	77.1
Eubosmina coregoni	0.49	0.54	53.2
E. longispina	0.04	−0.10	1.2
Daphnia retrocurva	0.78	0.41	77.7
D. galeata	0.29	0.42	26.1
Ceriodaphnia lacustris	0.70	0.38	63.4
Diacyclops thomasi	0.62	−0.26	45.2
Tropocyclops p. mexicanus	0.25	0.49	30.3
Limnocalanus macrurus	−0.45	0.31	29.9
Diaptomus oregonensis	0.49	0.17	26.9
Eurytemora affinis	0.48	0.33	33.9
Keratella cochlearis	0.81	−0.44	85.0
K. quadrata	0.24	−0.77	65.1
K. heimalis	−0.30	−0.48	32.0
Polyarthra sp.	0.86	−0.39	89.2
Kellicottia longispina	0.23	−0.79	67.7
Trichocerca sp.	0.85	−0.06	72.6
Asplanchna sp.	0.46	−0.38	35.6
Filinia	−0.10	−0.15	3.3
Conochilus	0.68	−0.35	58.5
Synchaeta	−0.34	−0.52	38.6
Notholca	−0.81	−0.36	78.6
Ploesoma	0.56	−0.06	31.7
% total	32.3	16.7	

A comparison of vertical haul, grazing chamber, and

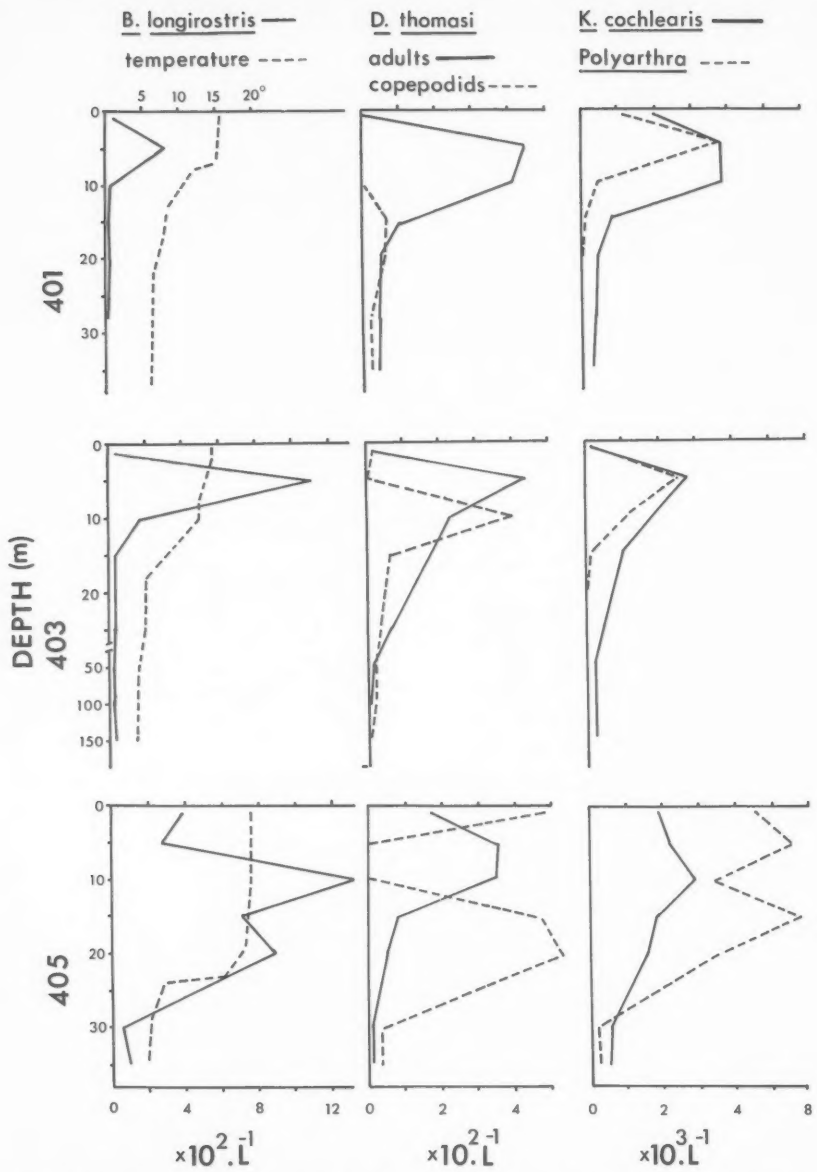

FIG. 4. Depth distribution of temperature and important zooplankton species during late August 1982. Stations and times are as for Fig. 3.

Schindler–Patalas trap estimates of zooplankton biomass is presented in Fig. 5. The Schindler–Patalas trap and the large Haney grazing chamber produced similar estimates of zooplankton biomass and gave higher estimates of biomass than the unmetered vertical hauls except during late summer. Net efficiency, judged by comparison with the chamber and trap results, fell below 20% during June. Figure 5 also illustrates that rotifers, which comprise the difference between "chamber" biomass and "chamber, crustacea only" biomass,are a significant component of metazoan zooplankton biomass.

Discussion

Lake Ontario still has a zooplankton fauna dominated by the cyclopoid *D. thomasi* and the cladoceran *B. longirostris*, although the latter is not abundant until August. This situation has persisted at least since 1967 (Patalas 1969), but probably was not always the case (McNaught and Buzzard 1973). Although the Laurentian Great Lakes in general, and Lake Ontario in particular, are unusual freshwater habitats in that their plankton biology is probably influenced by lake physics to

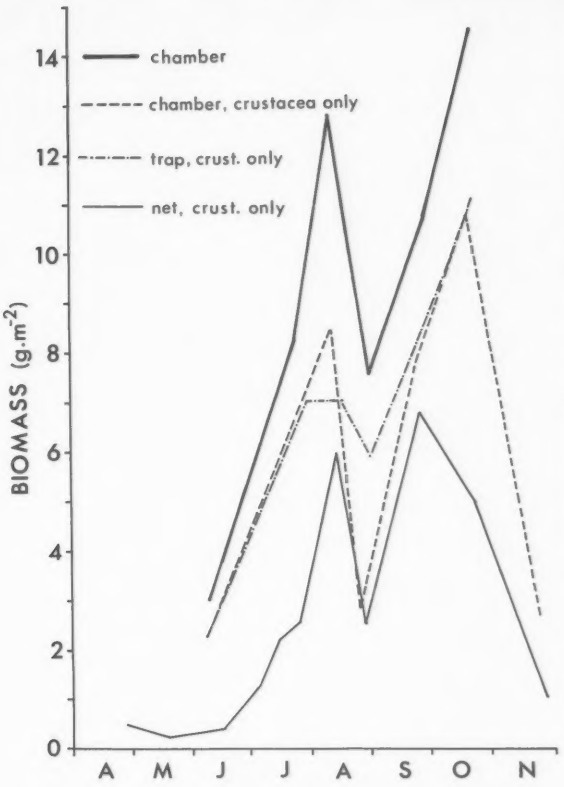

FIG. 5. Comparison of biomass estimates for metazoan zooplankton at station 403 during 1982 using a grazing chamber, a trap, and a net.

a greater extent than in most lakes, physics alone cannot explain the composition of their zooplankton fauna. The marked differences between northshore, midlake, and southshore stations in their seasonal cycles of stratification and warming produce differences in the timing of seasonal succession and in vertical distribution, but not in the basic species composition (Fig. 2, and see Patalas 1969). Indeed, *D. thomasi* and *B. longirostris* are among the most widely distributed zooplankters in North America, and are certainly not restricted to large lakes although *D. thomasi* may be a spring species in smaller bodies of water (e.g. Carter 1974). Nor is it tenable that the dominance of these species in Lake Ontario is attributable to eutrophication (Patalas 1972); Lake Ontario, with a total phosphorus concentration of about 12 $\mu g \cdot L^{-1}$ and a chlorophyll concentration of about 6 $\mu g \cdot L^{-1}$, is not eutrophic, nor are these species restricted to eutrophic lakes.

The most important factor determining the present zooplankton fauna of Lake Ontario may be the intense planktivory by fish. *Bosmina longirostris* is among the smallest planktonic Cladocera, and has displaced *Daphnia* in lakes where alewives have been introduced (Wells 1970). More recent studies in Lake Michigan have shown that even young-of-the-year alewives eat few *B. longirostris* (Brandt 1980) and, indeed, would incur very high energetic costs for doing so (Crowder and Binkowski 1983). *Eubosmina coregoni* and *C. lacustris* are also prominent in the plankton of Lake Ontario and are relatively small Cladocera. *Eubosmina coregoni* is slightly larger than, but otherwise similar to, *B. longirostris* and may be more susceptible to fish predation (Stenson 1976). The most important *Daphnia*, *D. retrocurva*, is among the smallest of its genus.

Invertebrate predation may also be an important factor structuring the Lake Ontario community. *Daphnia retrocurva* has a pronounced tendency to develop helmets and has a prominent tail spine which may help it avoid *D. thomasi* predation. Although the late development of Cladocera in Lake Ontario could be due to low water temperatures, the abundance of cyclopoid predators early in summer may also be responsible for suppressing their increase. A detailed study of horizontal distributions by Patalas (1969) clearly shows *B. longirostris* and other Cladocera developing in the warmer east end of the lake and spreading westward. *Diacyclops* was more uniformly distributed over the lake in June and, in 1967, 1970, and 1982, reaches high densities before Cladocera appear. Cyclopoid predators appear to be important determinants of rotifer species composition in Lake Michigan (Stemberger and Evans 1984). *Mysis relicta* is a predator on Cladocera and has a high density in Lake Ontario (Johannsson et al. 1985). In lakes in western North America where it has been introduced, it has greatly reduced the abundance of Cladocera and delayed their appearance until midsummer when it ceases to migrate through the epilimnion (Rieman and Falter 1981). It also fails to penetrate the epilimnion of Lake Michigan in summer (McNaught and Hasler 1966; Bowers and Vanderploeg 1982).

Diacyclops thomasi, perhaps the most important planktonic crustacean in the lake, has been found to be resistant to fish predation in enclosure studies (D. McQueen, York University, Toronto, Ont., pers. comm.). The other important cyclopoid, *Tropocyclops prasinus mexicanus*, is smaller and may outnumber *D. thomasi* at times (e.g. offshore eastern Lake Ontario in September, Patalas 1969) and inshore waters of Georgian Bay (Carter 1972, and work in progress).

If the present fauna is a product of species interactions, and especially involving planktivorous fish, then one might expect differences between the fauna of the 1960's and early 1970's and the fauna we found in 1982. Our analysis (Fig. 2) illustrates that the zooplankton community has changed very little in species composition or in the timing of species succession between 1970 and 1982. The reduced abundance of *Daphnia* nearshore in 1982 may be the result of frequent upwelling in that year (Simons and Schertzer 1987). Although our estimates of biomass (Fig. 5) are obviously crude, they are of the same order, although slightly lower, than those by Watson and Carpenter (1974); they calculated lake averages and expressed biomass of numbers per cubic metre in the top 50 m. Their maximum biomass for 1970, multiplied by 50 to convert to biomass per square metre, is very similar to the September maximum shown in Fig. 5 for net hauls, crustacea only (7.85 $g \cdot m^{-2}$). It should also be noted from Fig. 5 that the unmetered net severely underestimated biomass during spring, early summer, and fall, when colonial diatoms are abundant, and that rotifers are a serious omission from biomass calculations.

An important question which arises from these data is the importance of invertebrate predation in delaying and limiting the development of the cladoceran fauna, and whether the invertebrate predators will be positively affected by further reductions in planktivore biomass. This is related to the larger question as to whether the balance between large and small Cladocera is determined by vertebrate predators and competition, or vertebrate and invertebrate predators (Lane 1978). If planktivorous fish continue to decline, large-bodied Cladocera

may come to dominate the late-summer zooplankton fauna, as they have done in Lake Michigan. *Bosmina* is more vulnerable to *Mysis* than *D. retrocurva* or *D. geleata* (Bowers and Vanderploeg 1982). Whether they could appear earlier in the presence of similar or higher numbers of invertebrate predators is doubtful. As planktivory by fishes declines, perhaps the role of herbivore in the spring and early summer plankton will pass from rotifers and ciliates (see Fig. 5; Taylor and Heynen 1987; Nauwerck 1978) to calanoid copepods. If these interpretations of the zooplankton fauna of Lake Ontario and how it changes are correct, they suggest yet another avenue through which human activity interacts with water quality and the biological integrity of this important ecosystem.

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Seasonal and Vertical Distribution of Ciliophora in Lake Ontario

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Taylor, W. D., and M. L. Heynen. 1987. Seasonal and vertical distribution of Ciliophora in Lake Ontario. Can. J. Fish. Aquat. Sci. 44: 2185–2191.

Ciliated protozoa were sampled at discrete depths from April through October 1982 at a nearshore (38 m depth) and an offshore (178 m depth) station in Lake Ontario. Nearshore, ciliates increased from less than 1 $g \cdot m^{-2}$ in early spring to a maximum of about 5 $g \cdot m^{-2}$ (wet weight) inside the thermal bar in late May and early June. Summer values varied around 2 $g \cdot m^{-2}$ and declined even further in October. Offshore ciliate biomass was relatively constant; the observed range was only 2.8–6.5 $g \cdot m^{-2}$. Early spring biomass was much higher than nearshore, suggesting that a significant population persists through the winter, but the spring biomass increase was later. Although biomass concentration was greater in the epilimnion, on an areal basis most of the population resided in the hypolimnion. The hypolimnetic population declined during the summer period of thermal stratification. The observed number of taxa ranged from 15 to 30 per sample. Most had distinct seasonal and vertical distributions. The majority appear to be algivores, but the role of ciliates in the food web of Lake Ontario remains largely unknown. Their biomass is comparable with that of metazoan zooplankton, and with their higher metabolic rates, they probably perform much more of the total grazing.

Des échantillons de protozoaires ciliés ont été prélevés à des profondeurs discrètes, d'avril à octobre 1982, près du rivage (38 m de profondeur) et au large (178 m de profondeur) dans le lac Ontario. Près du rivage, le poids des ciliés a augmenté de moins de 1 $g \cdot m^{-2}$ au début du printemps à un maximum d'environ 5 $g \cdot m^{-2}$ (poids humide) dans la barre thermique à la fin de mai et au début juin. Les valeurs estivales ont varié autour de 2 $g \cdot m^{-2}$, avec un déclin plus marqué en octobre. La biomasse ciliée au large est restée relativement constante, variant seulement entre 2,8 et 6,5 $g \cdot m^{-2}$. La biomasse au début du printemps était bien supérieure à celle près du rivage, ce qui indique qu'une importante population a survécu pendant l'hiver, mais que la biomasse du printemps a augmenté plus tard. Bien que la concentration de la biomasse ait été plus grande dans l'épolimnion, par unité de surface, le gros de la population a résidé dans l'hypolimnion. La population hypolimnétique a décliné pendant la période estivale de stratification thermique. Le nombre observé de taxa a varié de 15 à 30 par échantillon. La majorité semble être algivore, mais le rôle des ciliés dans le réseau alimentaire du lac Ontario reste très peu connu. Leur biomasse est comparable à celle du zooplancton mésozoaire et, à cause de leur métabolisme plus élevé, ils sont probablement responsable d'une proportion beaucoup plus importante du broutage total.

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Recent developments in limnology have focussed attention on ciliates as important members of freshwater zooplankton communities, including those in the Laurentian Great Lakes. We now appreciate that nannoplankton and picoplankton are important primary producers (Caron et al. 1985; Pick and Caron 1987) and that protozoa are important consumers of that production (Taylor 1984; Pick and Caron 1987). Although early studies concentrating on crustacean zooplankton reported the presence of loricate *Codonella* and attached or colonial peritrichs (see Watson 1974), and although epizootic suctoria have been recently documented (Evans et al. 1979, 1981), our lack of quantitative population estimates for ciliates remains a major gap in our knowledge of Great Lakes fauna.

The Laurentian Great lakes have undergone major shifts in zooplankton size distribution (toward the small), probably as a result of changes in fish species composition (Wells 1970), and may now be undergoing a reversal of these changes (Jude and Tesar 1985). Such shifts are related to changes in phytoplankton composition and biomass (McNaught and Scavia 1976; Stenson et al. 1978; Shapiro and Wright 1984), and so ciliates, close to the small end of the zooplankton size spectrum, may be an important indicator group in these changing ecosystems.

During the Lake Ontario Nutrient Assessment Study (LONAS) cruises in 1982, we obtained ciliate samples from an inshore and offshore station during April through October. These collections were accompanied by detailed chemical, physical, and biological measurements (see other papers in this issue). This report details the seasonal and vertical distribution of abundance and biomass of ciliates for both stations.

Materials and Methods

Samples were collected from discrete depths at two stations using Niskin bottles mounted on a rosette sampler. Station 403 was near midlake (depth = 178 m), while station 401 was about

TABLE 1. Seasonal and vertical distribution of Ciliophora at offshore station 403 during 1982. Abundance is given in numbers·mL^{-1} and the integrated areal total is in billions·m^{-2}. Station depth is 178 m.

	Date (day/month)									
Depth (m)	7/4[a]	28/4	18/5	9/6	28/6	13/7	8/8	24/8	22/9	14/10
1	—	5.7	4.2	5.0	8.2	11.3	22.6	10.4	17.2	18.5
5	5.3	6.0	6.0	3.4	8.9	13.4	34.3	14.7	15.7	20.2
10	—	—	—	4.1	9.2	6.5	40.2	15.5	13.4	18.1
15	—	9.4	5.8	5.2	9.7	7.4	15.2	12.9	17.9	16.9
25	5.2	9.2	4.5	4.2	6.6	9.2	6.6	6.5	6.2	16.9
50	6.6	8.4	7.9	4.2	8.6	6.2	6.4	3.5	4.6	4.1
75	—	8.0	6.8	4.8	7.1	6.8	4.8	2.0	2.6	—
100	5.6	7.0	6.4	4.4	7.3	8.3	4.8	2.6	2.4	4.0
125	—	9.4	6.9	4.1	5.9	7.5	5.1	1.9	2.5	—
150	—	9.7	6.8	3.1	5.0	5.0	5.1	—	2.6	3.3
168	—	8.3	6.7	3.9	5.1	6.1	5.5	2.4	3.3	3.1
176	—	7.2	6.6	4.3	4.3	6.5	4.9	2.7	2.8	4.1
Areal total	1.02	1.50	1.17	0.74	1.22	1.29	1.39	1.13	0.85	1.19

[a]Sample collected at station 404.

TABLE 2. Seasonal and vertical distribution of ciliate biomass at offshore station 403 during 1982. Biomass is given in μg·L^{-1} and the integrated areal total is in g·m^{-2}. Station depth is 178 m.

	Date (day/month)									
Depth (m)	7/4[a]	28/4	18/5	9/6	28/6	13/7	8/8	24/8	22/9	14/10
1	—	18	18	26	165	41	42	61	120	62
5	29	21	35	24	175	43	96	69	102	92
10	—	—	—	22	99	35	116	35	83	72
15	—	36	31	20	66	42	28	23	90	66
25	21	27	16	30	36	31	29	31	15	40
50	21	25	34	25	35	21	31	16	12	17
75	—	23	28	25	26	23	24	8	7	—
100	22	32	32	21	28	38	11	8	8	14
125	—	34	31	26	26	27	13	8	8	—
150	—	30	31	16	18	17	14	—	9	14
168	—	24	34	21	21	18	20	11	11	8
176	—	21	26	22	12	23	15	8	9	13
Areal total	4.5	4.9	5.3	4.2	6.5	4.8	4.5	2.8	3.4	4.1

[a]Sample collected at station 404.

4 km south of Cobourg, Ontario (depth = 38 m). Aliquots of 110 mL were fixed with 1 mL of Lugol's iodine within minutes of collection. Subsamples of 50 mL were later settled and examined with an inverted microscope. The usual counting regimen was to survey the entire chamber at 100 × magnification to count large species (approximately 40 μm or more in length) and then survey half of the chamber at 200 × by counting 500-μm transects every 1 mm across the chamber using a calibrated mechanical stage. Phase contrast optics were used. This procedure resulted in 100–600 specimens counted per sample, depending on their abundance.

There is no generally accepted fixation technique for planktonic ciliates. The Lugol's iodine we used as a preservative was satisfactory, although it makes large forms opaque and therefore difficult to identify. Using much less than 1.0% v/v results in poor preservation and the danger that delicate taxa are underestimated or damaged beyond recognition. We found mercuric chloride (Pace and Orcut 1981) to be a satisfactory alternative, although some forms, especially *Strobilidium* spp., are more often swollen or ruptured than with Lugol's iodine. We did not investigate using higher concentrations than Pace and Orcutt recommended.

With both of these fixatives, identification remains a problem. The system of kinetosomes and associated structures on which ciliate identification depends is not visible, and planktonic ciliates, especially the small forms, remain relatively ignored by ciliate taxonomists. We did prepare some protargol-stained specimens (Galigher and Kozloff 1964), but generally refrained from attaching species names to taxa based on comparison of unstained specimens with outdated descriptions of European material. However, it is likely, in our opinion, that the identification of most preserved but unstained specimens would be possible if appropriate descriptions existed. Other forms, such as *Tintinnidium* spp., were impossible for us to identify from unstained material even with recent redescriptions (Foissner and Wilbert 1979).

Ciliates were usually identified to genus; we consulted Corliss (1979) and Curds (1982) primarily. Although we

TABLE 3. Seasonal and vertical distribution of Ciliophora at nearshore station 401 during 1982. Abundance is given in numbers·mL^{-1} and the integrated areal total is in millions·m^{-2}. Station depth is 38 m.

	Date (day/month)									
Depth (m)	5/4	29/4	20/5	8/6	28/6	15/7	12/8	23/8	23/9	20/10
1	—	19.1	26.9	21.1	15.1	12.5	11.7	12.0	19.8	3.5
5	5.8	20.2	25.4	17.1	9.2	16.7	12.8	21.2	20.6	3.0
10	—	—	11.8	20.3	10.3	23.6	12.0	12.8	26.0	3.9
15	—	24.7	8.9	17.9	10.2	24.5	12.3	5.8	23.1	3.9
28	6.0[a]	19.2[a]	8.6	5.8	4.8	14.7	11.4	6.9	12.6	4.2
36	7.2	18.4	8.3	8.9	6.3	15.5	11.9	6.8	8.4	2.4
Areal total	233	785	474	517	317	698	455	361	672	138

[a]Sample collected at 25 m.

TABLE 4. Seasonal and vertical distribution of ciliate biomass at nearshore station 401 during 1982. Biomass is given in μg·L^{-1} and the integrated areal total is in g·m^{-2}. Station depth is 38 m.

	Date (day/month)								
Depth (m)	5/4	29/4	20/5	8/6	28/6	15/7	12/8	23/8	23/9
1	—	69	107	180	69	47	49	102	120
5	18	68	96	238	56	155	59	165	113
10	—	—	118	171	65	64	65	89	91
15	—	84	120	296	69	106	57	27	66
28	18[a]	69[a]	115	97	23	46	42	33	31
36	24	62	85	117	23	47	46	31	19
Areal total	0.73	2.71	4.10	6.85	1.85	2.88	1.97	2.27	2.36

[a]Sample collected at 25 m.

usually were not able to confidently assign names to species, we did differentiate among congeneric species whenever possible.

The first 10 properly oriented specimens of each taxon we encountered in a sample were measured at 400 × magnification to the nearest 1.25 μm. Volumes were estimated for each specimen and then averaged across taxa. When less than 10 specimens were encountered, estimates for adjacent depths were pooled. For September and October samples, only separate volume estimates for epilimnion and hypolimnion were used, rather than for each depth. Volumes for most taxa were approximated as prolate spheroids, while *Tintinnidium* was approximated as a cylinder and *Strombidium* volume was calculated with an empirically derived formula. Specific gravity was assumed to be 1.0 g·mL^{-1}, so biomass is expressed as wet weight.

Results

At the offshore station (LONAS station 403), areal abundance and biomass of ciliates were relatively constant (Tables 1 and 2). For both variables, the range was only about twofold. These areal estimates are dominated by the hypolimnetic population (greater than 37.5 m deep) at this deep station. The hypolimnetic population declined through the summer period of thermal stratification, and this more than balanced the higher biomass per litre in the epilimnion. Maximum biomass concentrations occurred in the epilimnion in late June and again in late August and September. The difference between epilimnetic and hypolimnetic biomass was greatest during this early fall period (e.g. September 22).

On the last sampling date, October 14, the biomass in the epilimnion was still high, reflecting that mixis had not yet occurred. On the previous April 7, before stratification began, biomass was similar at the four depths sampled and much higher than the hypolimnion values in October. This suggests that populations may persist through the winter, or that spring increase occurs even before April.

At the nearshore station (LONAS station 401), areal abundance and especially biomass were much more variable (Tables 3 and 4). Both were always lower because the depth was less. In summer, however, biomass concentration was usually higher at the nearshore station. Unlike at midlake, winter biomass appeared to be very low; April and November populations were small. Numbers, followed by biomass, peaked in spring. Whereas the offshore station had its peak epilimnetic biomass in late June, epilimnetic biomass had already declined nearshore. This may reflect that the nearshore stratified in early June, while the offshore was still isothermal (Simons and Schertzer 1987). In 1982, when these data were collected, offshore stratification may have been the result of the breakdown of the thermal bar and the displacement of the north-shore epilimnion southward (Simons and Schertzer 1987). Subsequent upwelling events are the cause of the greater variability of this station.

Samples contained from 15 to 30 recognizably different taxa, and probably a slightly larger number of species. The most abundant taxa were small (<30 μm). Small Kinetofragminophora (*Urotricha* spp., *Mesodinium* sp., and other forms we could not identify), scuticociliates (possibly *Cyclidium*), and oligotrichs (*Strobilidium* sp., or *Halteria*) were present in virtually all samples. The *Strobilidium* sp., and *Urotricha* sp., were as small as 10 μm in length, excluding cilia or ciliary organelles.

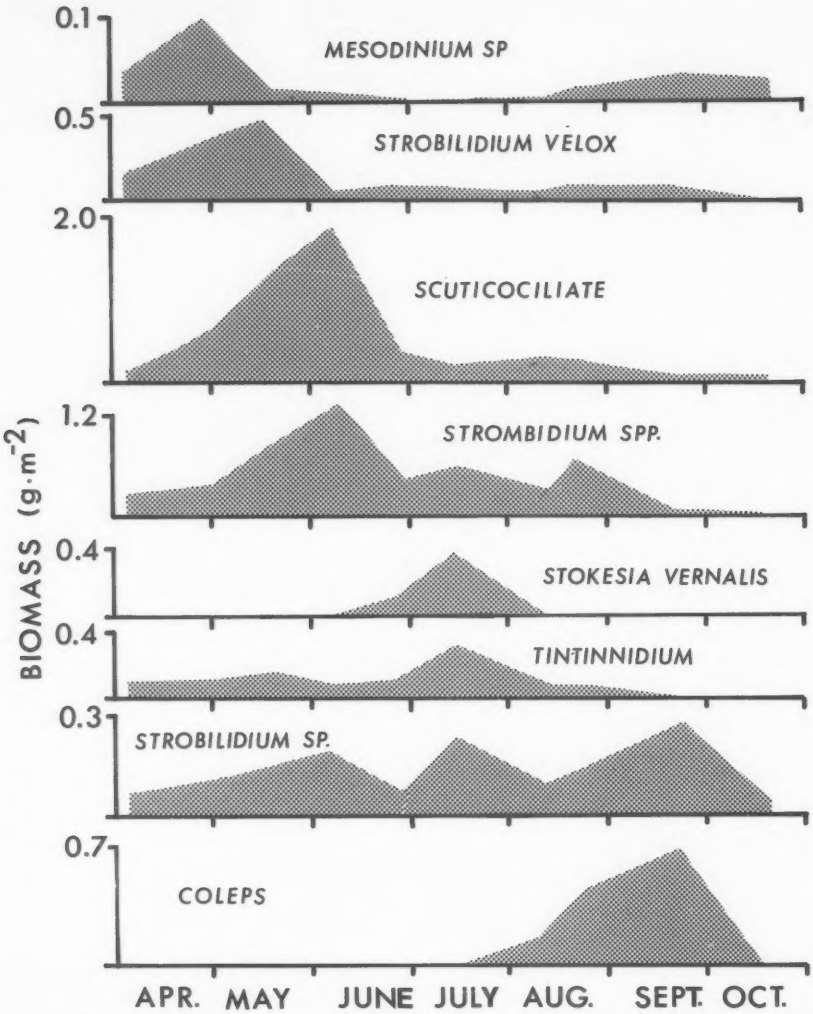

FIG. 1. Seasonal changes in biomass of important ciliate taxa at station 401 during 1982. Note that the scales are different.

Large species generally contributed most of the biomass and differed in their temporal distributions (Fig. 1). The offshore station had a similar succession, but was generally later than nearshore (Fig. 1), and hypolimnetic species were more important. In early April, samples from both sites were dominated by *Strobilidium velox*, a small *Strobilidium* sp., and a pleuronematine scuticociliate which is probably a new genus (D. Lynn, University of Guelph, Guelph, Ont., pers.comm.). *Strombidium* is most abundant in June and is represented by at least two species in Lake Ontario (G. Wehner, University of Waterloo, Waterloo, Ont., pers. comm.), but they were not counted separately. Among the spring fauna not shown in Fig. 1 is *Dileptus*. Specimens exceeding 1 mm in length were observed, and although their density was only $20 \cdot L^{-1}$ or less, they make a significant contribution to ciliate biomass.

Tintinnidium, small *Strobilidium* sp., and the unknown scuticociliate were abundant throughout the summer, largely in the hypolimnion (Fig. 2). Hypolimnetic species had broader seasonal maxima. *Halteria* appears to replace *Strobilidium* in the summer epilimnion. The recovery of ciliate biomass in the late summer epilimnion is due to *Coleps*.

The vertical distribution of ciliate biomass varies greatly among species, as demonstrated on June 28 for station 403 (Fig. 2). This is the date of the maximum observed areal biomass for this station (Table 2). *Stokesia vernalis*, which is bright green with zoochlorellae, is found only in the euphotic zone. *Strombidium* and *Codonella* have maxima at 15 m, at the base of the epilimnion. *Strombidium* also has algal symbionts, so its deep maximum is interesting. In a smaller lake, it was observed to migrate closer to the surface early and late in the day (Wehner 1985). The reason for the high biomass at this time, however, is that species like the unknown scuticociliate, *Tintinnidium*, *Strobilidium* sp., and *Akenasia* are abundant throughout the water column.

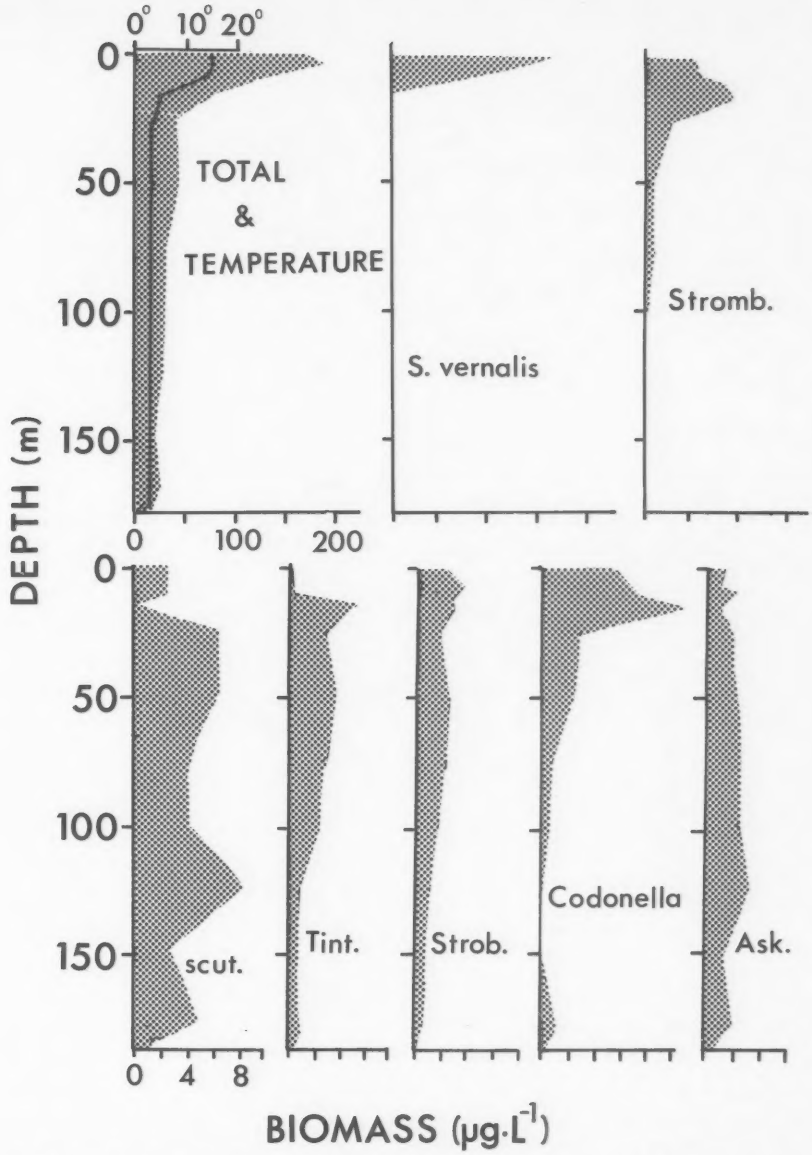

FIG. 2. Vertical distribution of biomass of important ciliates at station 403 on June 28. The lower row of graphs is at a different scale. Biomass is wet weight.

Discussion

The abundance and biomass of ciliates described here are much greater than previously reported in Great Lakes samples taken by net hauls or found in the contents of grazing chambers collected on 30-µm nylon screens during these same cruises (H. J. Fricker and A. Abbott, National Water Research Institute, Burlington, Ont., pers. comm.). Hunt and Chein (1983) enumerated ciliates in Cayuga Lake, New York State, after concentrating fixed samples on 35-µm screens. They reported lower densities than we found, but most of the ciliates we counted were less than 35 µm long.

The abundance and biomass of ciliates we observed are comparable with those found in other lake studies using settling chamber techniques. Pace and Orcutt (1981) found generally higher densities (over $10^5 \cdot L^{-1}$ in some cases) in more eutrophic and monomictic Lake Oglethorpe, although they include some protozoa other than ciliates in their counts. Densities of *Strombidium*, small oligotrichs, and *Vorticella* were comparable, but they found much higher abundances of small scutiociliates. Beaver and Crisman (1982) obtained similar densities of ciliates to Lake Ontario in oligotrophic Florida Lakes, as did Gates and Lewg (1984) in central Ontario lakes. In five lakes with similar total phosphorus concentrations (14–17 µg $P \cdot L^{-1}$),

Gates and Lewg reported mean ciliate biomass in the epilimnion of 65–240 $\mu g \cdot L^{-1}$ (after transforming their data assuming a specific gravity of 1.0 $pg \cdot \mu m^{-3}$). Similar ciliate populations were found in Jacks Lake by similar methods (Taylor and Lean 1981; Hamilton 1985). Jacks Lake is similar in trophic status to Lake Ontario. Our biomass and density estimates are considerably higher than reported for the oligotrophic Lunzer Untersee (Schlott-Idl 1984).

Most species appear to be algivores; although the feeding of planktivorous ciliates is poorly known, probable bactivores such as small scuticociliates, peritrichs, and *Halteria* were usually less than half of the biomass. Ciliate grazing may be directed primarily at autotrophs, and some of the most important ciliates, such as *Strobilidium velox* and *Stokesia vernalis*, consume algae too large for most cladoceran grazers. The large predator *Dileptus* is probably an important consumer of metazoan zooplankton. *Coleps* appears an unlikely planktonic ciliate; rather than being fast-swimming with powerful food-collecting organelles, it is slow and without any means of creating feeding currents or immobilizing prey. Bark (1981) also reported *Coleps* to be abundant in late summer, feeding on moribund *Ceratium*. We suspect that it somehow deters metazoan predators, possibly because of its calcareous plates. It often takes over laboratory cultures where small predatory invertebrates have consumed other ciliates.

The ciliate fauna also showed distinct patterns of vertical distribution. *Tintinnidium*, small scuticociliates, and the unknown pleuronematine were generally abundant in the hypolimnion, while many other forms, especially those with algal endosymbionts, are largely confined to the epilimnion during summer stratification. The higher concentration of ciliates in the epilimnion was expected, but the hypolimnetic population dominates the areal biomass estimates and must play an important role in the feeding of hypolimnetic crustacean zooplankton and in the fate of sinking particulate organic matter.

The areal biomass estimates of 2–7 $g \cdot m^{-2}$ wet weight are lower, but of the same order, as estimates for crustaceans during the same cruises (2–10 $g \cdot m^{-2}$ (dry weight), Taylor et al. 1987). Gates et al. (1982) suggested a dry/wet weight ratio for ciliates of 0.279. During June and July, crustacean grazers were few at our stations; therefore, ciliates and rotifers were probably the major grazers. Carbon fixation at optimum light was about 8 $\mu g\, C \cdot L^{-1} \cdot h^{-1}$ during 1982 (Lean et al. 1987), so the observed ciliate biomass of 50–250 $\mu g \cdot L^{-1}$ or 5–25 $\mu g\ C \cdot L^{-1}$ could process all of the daily production. Generation times for larger ciliates were estimated as 1–2 d (Taylor 1984).

The cyclopoid *Diacylops thomasi* is very abundant in Lake Ontario, and its population largely develops during June and July before Cladocera become abundant (Fricker and Abbott 1985). It probably is an important link between microzooplankton and other trophic levels.

The role of ciliated protozoa in Lake Ontario, and lakes in general, is far from clear. Their prey, and their predators, are largely a matter of speculation. But given their biomass, and relatively high metabolic rates compared with other zooplankton (Taylor 1984; Banse 1982; Shuter et al. 1983), it is clear that they must be included in any comprehensive study of the Lake Ontario plankton community.

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Spatial Heterogeneity of Nutrients and Organic Matter in Lake Ontario

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Neilson, M. A., and R. J. J. Stevens. 1987. Spatial heterogeneity of nutrients and organic matter in Lake Ontario. Can. J. Fish. Aquat. Sci. 44: 2192–2203.

During spring, Lake Ontario was vertically homogeneous except for the bottom 2 m where soluble reactive silica (SRS) and temperature (TEMP) were significantly ($p < 0.05$) elevated and dissolved oxygen was depleted. With stratification, soluble reactive phosphorus (SRP) and total filtered phosphorus, SRS, and nitrate-plus-nitrite were depleted in the epilimnion due to phytoplankton uptake. Total unfiltered phosphorus (TP) and ammonia (NH_3) exhibited higher epilimnetic concentrations, the former being attributed to tributary inputs which were maintained throughout the stratified period, even though inputs from Niagara River served to dilute the epilimnion. Increased levels of TP, SRP, and SRS were also evident within the nepheloid layer. Horizontal distributions of TP and NH_3 were governed by point-source inputs throughout the study period. Distributions of the soluble nutrients were governed by phytoplankton uptake in the spring, point/nonpoint inputs and upwelling in the summer, and differential breakdown of stratification in the fall. Spring distribution of particulate organic matter (POM) was strongly related to nutrient availability and water column stability, while phytoplankton species composition determined fall POM distribution. Significantly higher ($p < 0.05$) POM levels, detrital content, and productivity were observed nearshore of the thermal bar.

Au printemps, les eaux du lac Ontario étaient verticalement homogènes sauf pour les 2 m au-dessus du fond où les teneurs en silice réactive soluble (SRS) et la température (TEMP) étaient nettement plus élevées ($p < 0,05$) et l'oxygène dissous était abaissé. La stratification a amené un épuisement des teneurs en phosphore réactif soluble (PRS) et total filtré, en SRS et en nitrate–nitrite dans l'épilimnion par suite de la captation par le phytoplancton. Les teneurs en phosphore total non filtré (PT) et en ammoniac (NH_3) étaient plus élevées dans l'épilimnion; dans le cas du premier, ceci est attribué aux charges des tributaires maintenues pendant toute la période de stratification malgré une dilution par les eaux épilimnétiques des charges provenant de la rivière Niagara. Des teneurs accrues en PT, PRS et SRS étaient aussi évidentes dans la couche néphéloïde. La distribution horizontale du PT et du NH_3 était soumise aux charges ponctuelles pendant toute la période expérimentale tandis que la distribution des bioéléments solubles était régie par la captation phytoplanctonique au printemps, les charges ponctuelles ou non et les remontées d'eau profonde en été, et la disparition différentielle de la stratification en automne. La distribution printanière de la matière organique particulaire (MOP) était fortement liée à la disponibilité de bioéléments et à la stabilité de la colonne d'eau tandis que la composition spécifique du phytoplancton déterminait la distribution de la MOP en automne. Les teneurs en MOP, les concentrations de détritus et la productivité étaient nettement plus élevées ($p < 0,05$) du côté côtier du seuil thermique.

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Spatial heterogeneity has been recognized as important in the resistance of lakes to eutrophication (Imboden 1974; Imboden et al. 1983). Considering the level of effort being expended to reduce the extent of eutrophication of Lake Ontario, it becomes of considerable importance, then, to understand the distribution of chemical and biological constituents within the lake, as well as the underlying mechanisms responsible.

Previous work on horizontal and vertical patterns of nutrients and particulate organic material in Lake Ontario has been limited in scope. For example, Gachter et al. (1974) and El-Shaarawi and Kwiatkowski (1977) described the horizontal distribution of selected variables in the surface waters, but provided no information as to their distribution throughout the water column. Dobson's (1984) atlas encompassed data collected on Lake Ontario from 1967 to 1982 and used an illustrative approach to highlight selected chemical/biological trends in time and their vertical and, to a lesser extent, spatial distributions. Sweers (1969), reporting on 1966 and 1967 Lake Ontario data, provided horizontal and vertical distribution patterns and seasonal changes, but only for temperature, pH, conductivity, oxygen, and hardness, while Shiomi and Chawla (1970), using year-round, lakewide data, restricted their discussion to phosphorus, nitrogen, and silica. Other authors have described only the distribution of phytoplankton biomass in Lake Ontario (Munawar and Nauwerck 1971; Vollenweider et al. 1974; Munawar et al. 1974; Stadelmann et al. 1974; Glooschenko et al. 1974).

Some effort has been directed towards developing models to simulate observations along a north-south transect at the 78°W

longitude in Lake Ontario. Chemical and biological distributions along this transect during the transition period between spring and summer were described in terms of biological and physical processes by Scavia and Bennett (1980) using a two-dimensional model. Seasonal distributions of phosphorus and nitrogen at a midlake station on this transect were incorporated into the nutrient cycle model derived by Stadelmann and Fraser (1974) to estimate rates of sedimentation out of the epilimnion and regeneration within the epilimnion. They stressed, however, that their findings had limited application for describing biochemical processes in the whole lake and that better spatial coverage was required.

The distribution of nutrient variables in the offshore waters of Lake Ontario is the net result of anthropogenic inputs, thermal structure, regeneration within the water column, and assimilation by phytoplankton. Considerable insight into the relative importance of these factors can be obtained by examining an extensive series of variables over a large area. However, variable-by-variable investigations are both tedious and, due to complicating factors such as spurious correlations, can provide misleading information. Utilization of more advanced statistical techniques allows the investigator to focus on determinants of variable distribution.

We used several statistical approaches to describe the vertical and horizontal distributions of variables in Lake Ontario, with emphasis on nutrients, particulate organic carbon and nitrogen, and chlorophyll *a*, highlighting such phenomena as thermal bar formation and stratification. As 1981 and 1982 were designated intensive sampling years on Lake Ontario in the Great Lakes International Surveillance Plan (International Joint Commission 1980), a greater amount of data exists for these years; thus, attention will be focused primarily on this period.

Methods

Data Collection

At approximately monthly intervals from March to December (1981) and March to November (1982), 21 cruises were conducted on Lake Ontario to measure concentrations of the following variables throughout the water column: temperature (TEMP), specific conductance (COND), alkalinity (ALK), total unfiltered and filtered phosphorus (TP, TFP), filtered ammonia (NH_3), filtered nitrate-plus-nitrite (NO_3), soluble reactive phosphorus and silica (SRP, SRS), dissolved oxygen (DO_2), particulate organic carbon and nitrogen (POC, TPN), chlorophyll *a*, corrected for phaeophytin (CHLA), and the filtered major ions Cl^-, SO_4^{2-}, Na^+, K^+, Mg^{2+}, and Ca^{2+}. Dissolved inorganic nitrogen (DIN) was calculated as the sum of filtered nitrate, nitrite, and ammonia.

Two sampling patterns were employed: either all 19 variables or a reduced set of 8 variables (TEMP, COND, TP, DO_2, POC, TPN, CHLA, Cl^-) were measured. The full complement of variables were only measured on spring cruises (March, April), two summer cruises (August 1981, September 1982), and during November.

Ninety-four stations provided coverage of the lake with the higher density of stations being nearshore where variability is the greatest (Lee 1975; Haffner et al. 1984). CHLA, POC, and TPN samples were obtained with a 0–20 m integrator (Schroeder 1969). For all other variables, sampling depths during nonstratified conditions were 1, 10, and 25 m and 10, and 2 m above bottom. During stratified conditions, sampling depths were 1 m, 1 m above the upper knee of the thermocline, 1 m below the lower knee of the thermocline, and 10 and 2 m above bottom.

Discrete samples were collected with a Rosette Multi-bottle Array Mark V sampler (General Oceanics Limited, Florida), interfaced with a Guideline EBT (electrobathythermograph) probe which simultaneously records temperature and depth. Soluble nutrients (SRP, NH_3, NO_3), COND, and DO_2 analyses were conducted on board ship immediately after collection. Samples for the remaining variables were preserved and analyzed as described in the *Analytical Methods Manual* (Department of the Environment 1979) by the Water Quality Branch, Burlington, Ont.

Data Analysis

To investigate the assumption of homogeneity of the water column during isothermal (spring) conditions, surface (1 m) values of TEMP, COND, DO_2, ALK, TP, TFP, NH_3, Cl^-, TFN, NO_3, and SRS were compared with 10 m, 25 m, and bottom-minus-2 m measurements at each station for 1981 and 1982 spring cruises using a paired *t*-test. Epilimnetic and hypolimnetic concentrations of TP, SRP, NH_3, SRS, NO_3, DO_2, and COND, during the stratified period, were compared using a nonpaired *t*-test. Results obtained from sampling conducted within the range of the nepheloid layer (bottom-minus-10 m and bottom-minus-2 m) were then excluded and the *t*-test reapplied. Differences were considered significant at $p < 0.05$.

Volume- and area-weighted mean concentrations were determined from application of the program ALDAR (Neilson et al. 1984). This program produces area- and volume-weighted statistics for predefined layers within a lake based on vertical interpolation of data collected at discrete sampling locations. Gridded representations of the lake, which include bathymetric data, are used to calculate within-layer weighted concentrations and to produce the overall mean.

To discern possible processes governing horizontal variability, various combinations of nutrient, particulate organic matter (POM), and chemical variables were subjected to principal components analysis (PCA). Analyses were conducted on the raw data files using the method of principal factoring without iteration, with quartimax rotation, and a minimum eigenvalue of 1.0. Linear regression was used as an additional means of investigating possible interrelationships among the variables. All statistical analyses were completed using the *Statistical Package for the Social Sciences* (Nie et al. 1975).

Results and Discussion

Vertical Distribution

Spring

It has been reported (Shiomi and Chawla 1970; Scavia and Bennett 1980; Bartone and Schelske 1982; Stevens et al. 1985) that nutrient concentrations appear to be vertically homogeneous during spring isothermal conditions, suggesting that wind-driven turbulence is of sufficient magnitude to effect complete vertical mixing of the water column. To investigate this previously untested hypothesis, a paired *t*-test was applied to the four spring cruises for 1981 and 1982; there was no significant difference between surface and discrete depth data for 104 of the 132 comparisons. Where statistically significant differences did occur, more than two thirds were surface to bottom-minus-2 m comparisons. In the bottom-minus-2 m

TABLE 1. Comparison of mean epilimnetic (EPI) and hypolimnetic (excluding
column) water characteristics observed during the summer months in Lake Ontario.

Date (d/mo/yr)		*n*	Temperature (°C)	Specific conductance (μS)	Dissolved oxygen ($mg \cdot L^{-1}$)	pho (m
15/06/81–	EPI	134	13.13±2.44	328.3±12.2	12.81±1.11	0.01
19/06/81	Hypo − B	48	4.24±0.41	333.9±6.6	13.30±0.24	0.01
	Hypo + B	180	4.18±0.64	333.0±8.9	13.01±0.53	0.01
13/07/81–	EPI	152	18.97±3.10	315.4±10.5	10.93±1.28	0.01
17/07/81	Hypo − B	46	4.33±0.79	329.8±6.6	12.72±0.88	0.01
	Hypo + B	164	4.22±0.85	328.3±5.6	12.41±0.93	0.01
10/08/81–	EPI	167	20.76±4.35	309.9±14.7	9.63±0.72	0.01
14/08/81	Hypo − B	50	4.35±0.63	334.7±7.8	12.15±0.85	0.01
	Hypo + B	157	4.22±0.68	330.9±6.5	11.87±0.88	0.01
14/09/81–	EPI	195	18.48±1.57	313.1±8.4	9.99±1.09	0.01
18/09/81	Hypo − B	40	4.26±0.50	331.0±7.7	12.29±0.99	0.01
	Hypo + B	139	4.26±0.78	329.7±6.0	11.72±1.00	0.01
12/07/82–	EPI	141	16.59±2.41	317.5±11.2	11.68±0.96	0.01
16/07/82	Hypo − B	51	4.40±0.61	330.7±21.5	13.42±0.40	0.01
	Hypo + B	178	4.30±0.83	331.3±18.9	13.00±0.73	0.01
16/08/82–	EPI	154	18.99±3.44	319.4±10.1	9.90±1.03	0.01
20/08/82	Hypo − B	47	4.32±0.52	337.9±14.1	12.48±0.94	0.01
	Hypo + B	163	4.20±0.59	336.3±12.1	12.00±1.08	0.01
13/09/82–	EPI	157	16.54±4.14	329.3±15.9	10.75±1.18	0.01
17/09/82	Hypo − B	46	4.14±0.30	358.0±14.2	12.89±0.56	0.01
	Hypo + B	151	4.17±0.67	355.3±13.5	12.20±1.05	0.01

xcluding (Hypo − B) and including (Hypo + B) the bottom 10 m of the water
e Ontario. All comparisons were significantly different ($\alpha = 0.05$).

d)	Total phosphorus ($mg \cdot L^{-1}$)	Soluble reactive phosphorus ($mg \cdot L^{-1}$)	Filtered ammonia ($mg \cdot L^{-1}$)	Soluble reactive silica ($mg \cdot L^{-1}$)	Filtered nitrate-plus-nitrite ($mg \cdot L^{-1}$)
11	0.016±0.005				
24	0.012±0.002				
53	0.014±0.004				
28	0.016±0.003				
88	0.011±0.002				
93	0.014±0.004				
72	0.019±0.008	0.002±0.001	0.014±0.015	0.177±0.144	0.074±0.045
85	0.010±0.002	0.004±0.002	0.006±0.009	0.317±0.147	0.364±0.044
88	0.013±0.005	0.007±0.004	0.005±0.007	0.573±0.320	0.375±0.044
09	0.015±0.003				
99	0.010±0.002				
00	0.014±0.004				
96	0.014±0.003				
40	0.011±0.002				
73	0.013±0.004				
03	0.015±0.002				
94	0.010±0.002				
08	0.013±0.004				
18	0.016±0.003	0.001±0.001	0.009±0.013	0.188±0.110	0.151±0.069
56	0.010±0.002	0.003±0.002	0.002±0.003	0.362±0.133	0.373±0.034
05	0.014±0.005	0.007±0.005	0.003±0.003	0.743±0.451	0.392±0.035

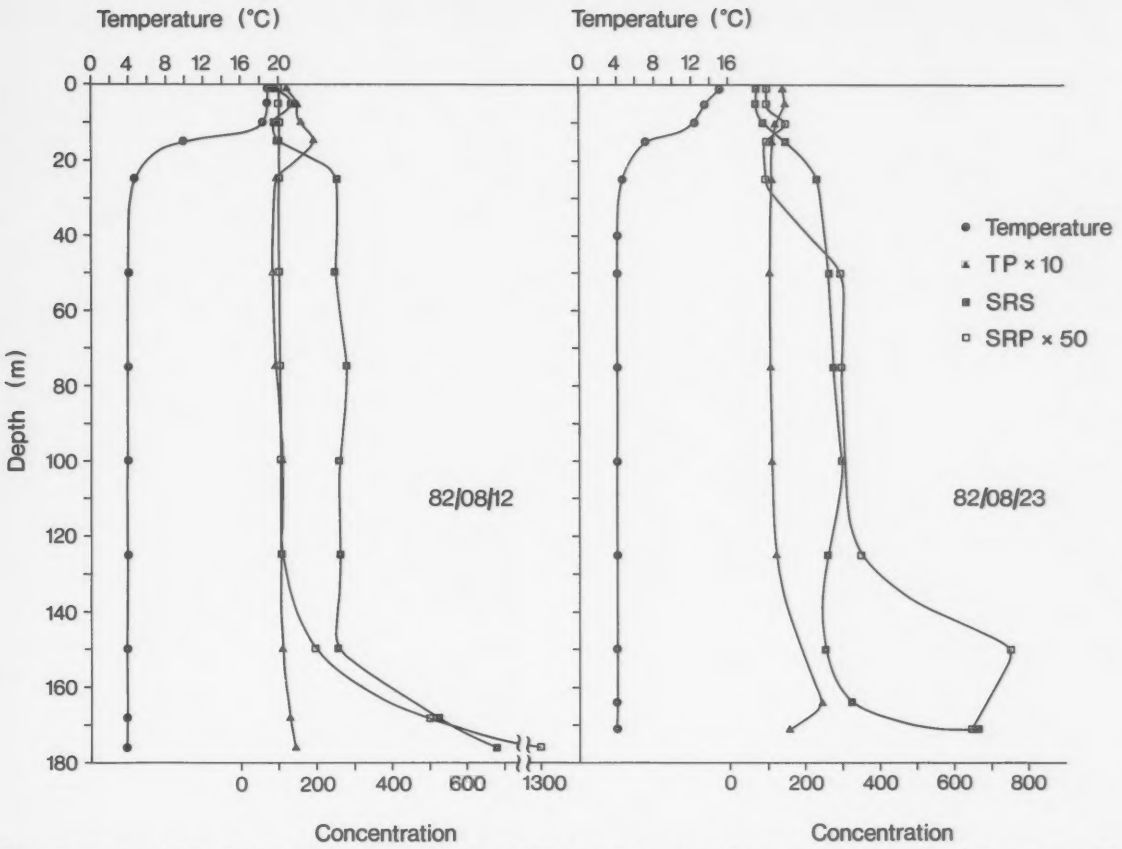

FIG. 1. Summer vertical distributions of temperature, TP, SRP, and SRS at a midlake station. All concentrations are in $\mu g \cdot L^{-1}$. Data courtesy of D. R. S. Lean (National Water Research Institute, Burlington, Ont.).

samples, DO_2 exhibited significantly reduced (-0.3 mg·L^{-1}) levels, while, except for early April (1981), TEMP was significantly higher (+0.3–0.5°C). This suggests that there is a relatively quiescent layer close to the bottom of the lake where water quality is significantly altered by sediment regeneration and/or uptake processes. SRS bottom 2 m concentrations during early April (1982) demonstrated the greatest mean deviation from surface values (28.3%); of the others, the actual mean difference was always less than 5%. Except for SRS, our data were consistent with the hypothesis of an isothermal, chemically homogeneous water column.

Stratification

While the onset of stratification in Lake Ontario begins early in May in the nearshore waters, complete thermal stratification is not fully established until late in June. Once established, surface inputs become essentially confined to the epilimnion, and marked changes in the distribution of variables in the water column become evident. Epilimnetic levels of COND, DO_2, SRP, SRS, and NO_3 were all significantly lower than hypolimnetic levels, based on a nonpaired t-test. Contrary to most lakes, however, epilimnetic TP and NH_3 concentrations were significantly higher than those of the hypolimnion.

Since in this comparison unweighted mean values were used, it was necessary to consider the biasing effect of the nepheloid layer on hypolimnetic concentrations. The nepheloid layer in Lake Ontario, as reported by Sandilands and Mudroch (1983), is a bottom layer of turbidity evident at water depths >60 m wherein elevated levels of SRS and SRP have been found. As this layer was reported to average 22 m in thickness in August and September 1982, determination of a mean hypolimnetic concentration inclusive of bottom-minus-10 m and bottom-minus-2 m data would be expected to be influenced by its presence. Exclusion of these data had no effect on mean hypolimnetic COND, DO_2, NH_3, or NO_3 or on the t-test results for these variables (Table 1). Similar to the results of Sandilands and Mudroch (1983), however, SRP and SRS concentrations were considerably higher within the bottom 10 m (Fig. 1). TP levels also were found to be substantially higher in this layer.

Sandilands and Mudroch (1983) attributed elevated SRS levels to dissolution of diatom frustules present in the nepheloid layer. A strong correlation ($r = 0.69$ and 0.63 for August 1981 and September 1982, respectively) between depth of the water column and bottom SRS levels supports the suggestion of Bartone and Schelske (1982) that the dissolution of diatoms and the resultant release of soluble silica occur mainly at the deepest soundings. Elevated levels of SRP were considered to be a result of the association of phosphorus with particles <0.45 μm in the nepheloid layer (Sandilands and Mudroch 1983) that, as postulated by Burns et al. (1976) for Lake Erie, are transported

TABLE 2. Eigenvalues, percent variance explained, and factor loadings for conductivity and ion PCA.

	August 1981		September 1982	
	Factor 1	Factor 2	Factor 1	Factor 2
Eigenvalue	4.67	1.03	4.48	1.28
% var. exp.	58.4	12.9	56.0	16.0
Loadings				
COND	0.77	0.36	0.43	0.64
ALK	0.89	0.12	0.12	0.91
SO_4^{2-}	0.42	0.54	0.85	0.17
Cl^-	0.48	0.76	0.91	0.26
Ca^{2+}	0.90	0.24	0.27	0.90
Mg^{2+}	0.53	0.55	0.25	0.67
K^+	−0.03	0.79	0.46	0.38
Na^+	0.43	0.80	0.92	0.28

as a resuspended organic floc within 2 m of the bottom. Elevated TP levels within the nepheloid layer would tend to support this hypothesis although increases in the soluble fraction are likely contributed by decomposition of settled material (Shiomi and Chawla 1970; Stadelmann and Fraser 1974) or diffusion of dissolved substances from the sediments.

Oxygen exhibited an orthograde distribution in the offshore waters of Lake Ontario, indicative of oligotrophic lakes (Wetzel 1975). Changes in epilimnetic DO_2 are principally a reflection of increasing surface temperatures such that mean percent saturation in the surface waters remained above 95% throughout the year, with maximum levels in excess of 120% during June 1981 and July 1982, coincident with the chlorophyll maximum. Hypolimnetic oxygen levels generally remained high throughout the summer, with percent saturation averaging greater than 90%. In the Kingston Basin, however, increased depletion was apparent within 10–20 m of the bottom, where saturation levels were as low as 58%, approaching those observed in the central basin of Lake Erie (Chapra and Dobson 1981).

Because of the immense volume of the hypolimnion in Lake Ontario (1.26×10^3 km^3), oxygen depletion, while measurable, was minimal. The volumetric hypolimnetic oxygen depletion (VHOD) rate was 8.4 and 11.3 $mg \cdot m^{-3} \cdot d^{-1}$ for 1981 and 1982, respectively, during the July–October period. This compares well with the average VHOD rate of 10.2 $mg \cdot m^{-3} \cdot d^{-1}$ for the period 1967–75 reported by Chapra and Dobson (1981). The Kingston Basin, in the northeastern region of the lake, exhibited a much greater VHOD rate, especially in the deeper regions (>25 m) near Adolphus Reach. Exchange with the Bay of Quinte, where a history of high VHOD rates exists (Minns and Johnson 1986), has resulted in VHOD rates in this region of 76.0 and 71.5 $mg \cdot m^{-3} \cdot d^{-1}$ for 1981 and 1982, respectively. At depths less than 25 m, more moderate depletion rates were observed, but the more rapid warming of these waters indicates considerable reoxygenation from overlying waters.

Because conductivity is directly proportional to the concentrations of the major ions, the depletion of COND in the epilimnion relative to the hypolimnion may result from a shift in distribution of the ions. As Mg^{2+}, Na^+, K^+, and Cl^- are relatively conservative ions, specific conductance will probably parallel the changes in Ca^{2+} and bicarbonate concentrations (Wetzel 1975). PCA of ion data with COND throughout the water column for summer cruises of 1981 and 1982 demonstrated that, indeed, ALK and Ca^{2+} showed a high degree of association with COND ($r_{123} = 0.63$ and 0.61, respectively), the resultant two factors accounting for 71 and 72% of the total variability (Table 2). When temperature was included among the list of variables, it loaded highly, but negatively, on the same factor as COND, ALK, and Ca^{2+} ($r = -0.92$ and -0.89 for 1981 and 1982), demonstrating the association between differences in their distribution and stratification of the water column.

Surface volume-weighted concentrations of both Ca^{2+} and ALK declined as the summer progressed as a result of the decreasing solubility of Ca^{2+} at warmer temperatures (Stumm and Morgan 1970). For example, 1981 volume-weighted mean surface concentrations declined from 39 mg $Ca^{2+} \cdot L^{-1}$ and 95 mg $CaCO_3 \cdot L^{-1}$ in the spring to 35 and 82, respectively, during the summer cruise. The precipitation of $CaCO_3$, previously observed by satellite imagery on Lake Ontario by Strong and Eadie (1978), effected a simultaneous decrease in epilimnetic COND from a 1981 spring 0–10 m volume-weighted mean of 340 μS to 310 μS in the summer. Theoretically, as a portion of the precipitating $CaCO_3$ is redissolved in the hypolimnion, an increase in Ca^{2+} should then be observed in the hypolimnion, but our data did not support this hypothesis; volume-weighted 40 m-to-bottom Ca^{2+} concentrations remained at 39 $mg \cdot L^{-1}$ throughout the year. Resolubilization may have occurred within the sediments as described by Zimmermann et al. (1987). Epilimnetic conductivity values, temperature corrected to 25°C, were consistently lower (average 5.2%) than those reported for the hypolimnion.

Shiomi and Chawla (1970) and Stadelmann and Fraser (1974) reported severe epilimnetic depletion of SRP, NO_3, NH_3, and SRS relative to spring concentrations. While a similar phenomenon was observed in 1981 and 1982, there were several notable differences. In 1972, spring offshore SRP concentrations averaged 14 $\mu g \cdot L^{-1}$, while summer epilimnetic values declined to approximately 1 $\mu g \cdot L^{-1}$. Hypolimnetic values, however, remained greater than 12 $\mu g \cdot L^{-1}$ throughout the stratified period. In contrast, spring 1982 SRP levels throughout the water column averaged only 5 $\mu g \cdot L^{-1}$. Summer epilimnetic SRP concentrations decreased to less than detectable levels (<0.20 $\mu g \cdot L^{-1}$) and hypolimnetic SRP also declined to less than 1 $\mu g \cdot L^{-1}$ in offshore waters.

Although present NO_3 concentrations are much greater than those exhibited in previous years (Stevens and Neilson 1987), epilimnetic DIN depletion, at 254 and 210 $\mu g \cdot L^{-1}$ for 1981 and 1982, respectively, was similar to that reported for 1969–71 (Dobson et al. 1974; Gachter et al. 1974). Whereas in 1970, summer epilimnetic DIN values were as low as 23 $\mu g \cdot L^{-1}$ compared with average spring concentrations of approximately 256 $\mu g \cdot L^{-1}$ (Shiomi and Chawla 1970), in 1982 (and similarly in 1981), spring levels of 360 $\mu g \cdot L^{-1}$ decreased to 150 $\mu g \cdot L^{-1}$ in the summer epilimnion. During August 1981 and September 1982, however, epilimnetic NH_3 concentrations were 13.6 and 9.2 $\mu g \cdot L^{-1}$, respectively, more than twice the spring values (5.5 $\mu g \cdot L^{-1}$). This epilimnetic increase coincided with a marked increase in zooplankton biomass (Johannsson et al. 1985; Lean and Knowles 1987; Taylor et al. 1987), suggesting that excretion by zooplankton during intense grazing periods may be responsible.

Seasonal patterns of TP concentrations in lakes typically show depletion in epilimnetic waters during summer stratification and accumulation due to phytoplankton uptake and subsequent sedimentation in the hypolimnion. At present, a very distinctive feature in Lake Ontario is epilimnetic TP levels

which are higher (range 28–82%) than hypolimnetic levels despite a mean (March–November 1981) particulate phosphorus sedimentation rate of 2.3 $mg \cdot m^{-2} \cdot d^{-1}$ (Rosa 1985). Summer epilimnetic TP concentrations during 1981 and 1982 did not differ from spring concentrations (15 $\mu g \cdot L^{-1}$), a phenomenon not observed in 1969 or 1972. This suggests that anthropogenic loadings of TP were maintained throughout the stratified period.

The TP load necessary to maintain a constant TP concentration in the epilimnion of Lake Ontario during the summer stratified period can be determined from existing data. For example, the initial mass of TP in the 0–10 m layer of the lake in July 1981 was 2910 metric tons (t). TP load from the Niagara River (July–September) was 410 t (K. Kuntz, Water Quality Branch, Canada Centre for Inland Waters, Burlington, Ont., pers. comm.), while losses from outflow were 600 t (A. Sylvestre, Water Quality Branch, Canada Centre for Inland Waters, Burlington, Ont., pers. comm.). A further loss of 2790 t was determined from TP sedimentation rate estimates of Charlton (1983) and Rosa (1985). Therefore, to maintain a constant TP concentration in the epilimnion during the July–September stratified period would require a load of approximately 2980 t.

Discharge from the Niagara River accounts for 80% of the total annual inflow to Lake Ontario and accounts for approximately 30% of the mean epilimnion volume from July to September, assuming that inflow (5.15×10^{10} m^3) is restricted to an epilimnion of 10 m average thickness. Daily measurements of inflow TP concentrations at the mouth of the Niagara River averaged only 12.4 and 12.8 $\mu g \cdot L^{-1}$ for the summer period during 1981 and 1982 (K. Kuntz, pers. comm.), suggesting that the Niagara River serves to dilute epilimnetic TP concentrations in Lake Ontario. It is apparent that inputs from sources other than the Niagara River must be significant during the stratified period.

Horizontal Distribution

Spring

During the spring isothermal period, surface temperatures were relatively uniform, averaging less than 1°C in early March 1982 to 2.5°C in early April 1981. Despite this uniformity of surface temperature, a distinct east-to-west increasing gradient in SRS was observed, similar to that reported by Shiomi and Chawla (1970) and Gachter et al. (1974). Midlake SRS concentrations averaged 360 $\mu g \cdot L^{-1}$, with highest levels noted along the western shoreline between Toronto and Niagara River (range 450–600 $\mu g \cdot L^{-1}$), while the Kingston Basin and the southern shore between the Niagara and Genesee rivers showed lowest concentrations (<200 and 215–310 $\mu g \cdot L^{-1}$, respectively). Inputs from the Genesee and Black rivers (454.0 and 457.0 $\mu g \cdot L^{-1}$, respectively) and the Bay of Quinte (1040.0 $\mu g \cdot L^{-1}$) seemed to have little impact on the general distribution of SRS in the lake.

In contrast with the results of Shiomi and Chawla (1970), neither spring NO_3 nor SRP concentrations, maximal at this time of year, demonstrated an east–west concentration gradient in 1981–82. Although NO_3 levels in the Kingston Basin and along the north shore as far west as Cobourg and nearshore from the Niagara to Genesee rivers were in the 240–300 $\mu g \cdot L^{-1}$ range, the rest of the lake exhibited uniform concentrations of 330–350 $\mu g \cdot L^{-1}$. SRP concentrations also remained fairly constant throughout the lake, being only slightly higher midlake (5–6 $\mu g \cdot L^{-1}$) and lowest in the Kingston Basin (<1 $\mu g \cdot L^{-1}$). When compared with the range of concentrations observed in 1969 (2.0–14.7 $\mu g \cdot L^{-1}$), the reductions in phosphorus loadings imposed in the Great Lakes since 1972 can be seen to have been effective in decreasing SRP levels.

Offshore NH_3 concentrations demonstrated little variability, with many regions of the lake exhibiting levels below the detection limit (<1.0 $\mu g \cdot L^{-1}$). Maximum concentrations (11–92 $\mu g \cdot L^{-1}$) were observed in the nearshore regions, especially near Toronto, Bay of Quinte, and Black River and along the southern shore between the Niagara and Genesee rivers (Fig. 2). Presumably the high concentrations noted along the south shore resulted from agricultural runoff because nitrification of ammonium in fertilizer is severely retarded in spring. Spring TP concentrations were similarly distributed, with inputs clearly definable from the Niagara, Genesee, Oswego, and Black rivers, Toronto, Hamilton, and Bay of Quinte, as well as along the south shore (Fig. 3). Offshore concentrations in 1981 ranged from 12.5 to 15.0 $\mu g \cdot L^{-1}$ and in 1982 from 11.0 to 13.0 $\mu g \cdot L^{-1}$.

PCA was applied to spring chemistry data to study interrelationships among the variables and to delineate possible processes governing the observed horizontal variability. The first factor, related to the relative concentrations of SRP, TFP, and SRS (and NO_3 in 1981), was responsible for more than one third the total explained variability. TP and NH_3 always loaded highly on the second factor. When the POM variables (POC, TPN, CHLA)[1] were incorporated into the PCA to determine if nutrient distributions could be related to biologically mediated changes (Table 3), SRP, TFP, and SRS (and NO_3 in 1981) loaded highly, but in contrast with POC, TPN, and CHLA on the first factor, and were responsible for more than 40% of the total explained variability for all cruises. As might be expected, therefore, the major factors determining nutrient distribution in the spring are phytoplankton growth and distribution of loadings.

Thermal bar formation

A feature specific to large lakes is the development of a narrow transition zone, the thermal bar, between the open and nearshore waters in spring. Shallow nearshore waters warm more rapidly than the open water mass and become stratified, while the open waters remain isothermal, typically well below 4°C (Simons and Schertzer 1987). The mid-May cruise of 1981 and the May and June cruises of 1982 were conducted during various stages of advancement of the thermal bar, the latter carried out at the time of maximum thermal bar development.

In inshore waters, elevated biomass is expected in response to warmer temperatures and higher rates of nutrient supply (Scavia and Bennett 1980). This hypothesis was tested using a *t*-test to compare concentrations of biomass indicators (CHLA, TPN, POC) across the 4°C isotherm (Table 4). All three biomass indicators proved significantly higher ($p < 0.05$) nearshore of the thermal bar, where chlorophyll levels were indicative of mesotrophic conditions, while the open waters remained in the oligotrophic range (Dobson et al. 1974). These findings are in contrast with those of Lake Huron where significantly higher nearshore POC and TPN concentrations have been reported (Stevens et al. 1985), yet no difference in CHLA concentrations across the thermal bar has been observed (Davis and Schelske 1976; Stevens et al. 1985). We feel this is due to differences in

[1]Data from early March (1982) were excluded since there were only 25 stations with complete data sets.

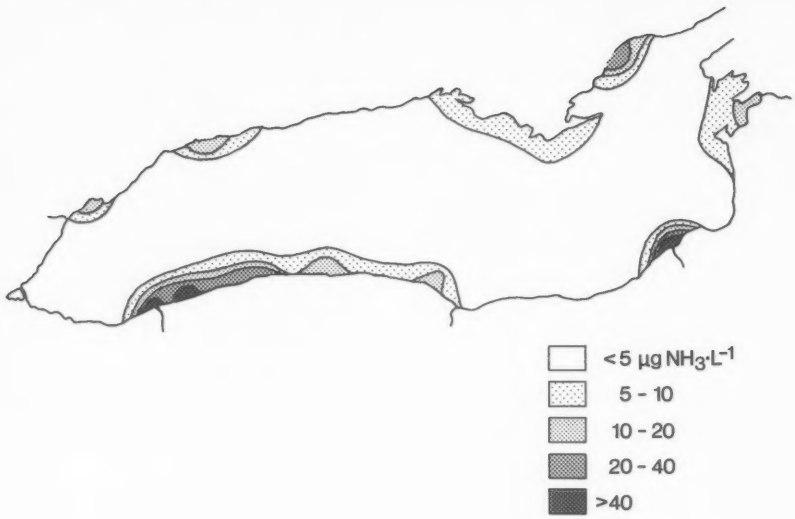

FIG. 2. Spring surface distribution of NH_3.

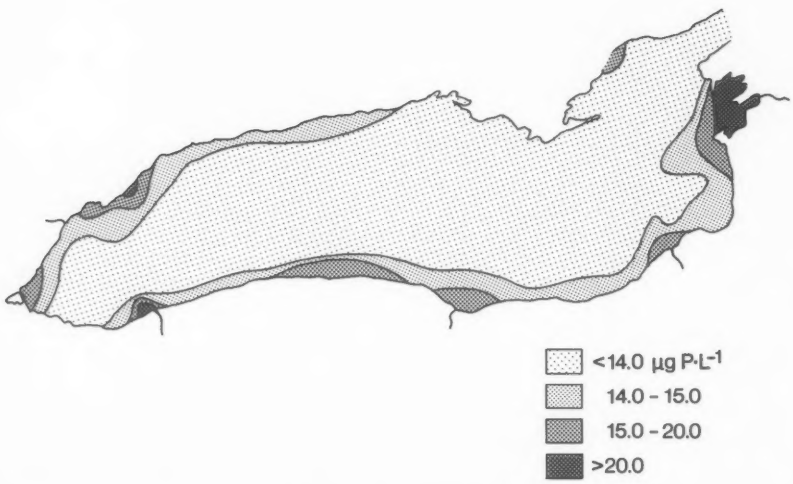

FIG. 3. Spring surface distribution of TP.

the seasonal cycles of biomass between the two systems. Lake Huron exhibits a unimodal chlorophyll *a* cycle in the open waters and a biomodal pattern in the nearshore. Lake Ontario's pattern is biomodal for both areas.

It was expected that increased productivity would accompany the elevated biomass levels observed in the nearshore. In the absence of direct measures of productivity, the regression of POC against CHLA, known as the *F* ratio (Strickland 1960), provides an estimate of the detrital component of the biomass (=intercept of the regression) (Steele and Baird 1965) and an indication of productivity (=slope of the regression) (Steele and Baird 1961). A *t*-test to compare *F* ratios across the 4°C isotherm was performed to test this hypothesis. The offshore data from June 1982 were not used because the regression equation was not significant (Table 4). Increased productivity, as evidenced by low POC/CHLA ratios (Halfon 1984), occurred in the nearshore region during May of 1981 and 1982.

Estimates of the nearshore detrital component, as determined from the *F* ratio intercept, for May 1981 and 1982 were 122.5 and 224.9 $\mu g \cdot L^{-1}$, respectively, compared with 14.7 and 58.4 $\mu g \cdot L^{-1}$ in the corresponding offshore waters. During both cruises, differences across the thermal bar were significant at the 95% level. Detritus constituted a much larger fraction of the total POC in the nearshore waters relative to offshore waters (27 compared with 9% in 1981, 60 compared with 36% in 1982). This would be expected given that allochthonous and littoral

TABLE 3. PCA of spring data with TPN, POC, and CHLA included.

	16/03/81–20/03/81				06/04/81–10/04/81			29/03/81–02/04/82		
	Factor 1	Factor 2	Factor 3	Factor 4	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3
Eigenvalue	6.02	2.50	1.22	1.04	5.84	2.82	1.71	5.39	2.77	1.85
% var. exp.	46.3	19.2	9.4	8.0	44.9	21.7	13.2	41.4	21.3	14.2
Loadings										
TEMP	0.78	0.10	0.12	−0.18	−0.51	0.64	0.10	−0.22	0.38	0.64
COND	−0.07	−0.81	0.03	0.17	0.11	−0.01	0.82	0.18	−0.37	0.65
ALK	0.04	0.09	0.06	0.93	0.11	−0.08	0.86	0.05	0.28	−0.65
TP	−0.15	0.83	0.30	0.06	−0.13	0.94	−0.20	0.32	0.84	0.05
SRP	0.96	−0.07	0.07	−0.06	0.94	−0.14	−0.02	−0.84	0.02	0.31
TFP	0.93	−0.01	0.09	−0.01	0.93	−0.06	−0.07	−0.86	0.25	0.06
NH_3	−0.15	0.84	−0.03	0.35	−0.27	0.79	0.11	0.05	0.77	−0.01
NO_3	0.84	0.15	0.34	−0.14	0.79	0.40	−0.17	−0.37	0.45	0.72
TFN	0.02	0.05	0.93	0.11	0.32	0.62	−0.25	−0.22	0.83	−0.15
SRS	0.61	0.21	0.56	−0.19	0.53	0.12	−0.73	−0.80	0.27	0.43
POC	−0.86	0.30	0.09	−0.11	−0.91	0.26	−0.06	0.93	0.16	0.01
TPN	−0.92	0.21	0.07	−0.10	−0.91	0.25	−0.08	0.95	0.26	−0.01
CHLA	−0.88	0.12	0.05	−0.21	−0.91	0.10	−0.10	0.95	0.02	0.07

TABLE 4. Changes across the thermal bar.

(a) *t*-test results comparing concentrations (x) of POC, TPN, and chlorophyll *a* (Chl) in the nearshore (NS) nd offshore (OS). All values are in $\mu g \cdot L^{-1}$.

	19/05/81–22/05/81			17/05/82–21/05/82			14/06/82–18/06/82		
	n	x	t^a	n	x	t^a	n	x	t^a
POC–NS	65	447.9±137.6	15.75	45	375.0±99.0	13.39	75	432.0±130.1	15.28
OS	25	161.2±31.6		43	160.1±41.1		12	176.0±25.7	
TPN–NS	65	72.1±23.4	13.67	45	61.3±16.2	12.81	75	72.7±21.1	12.37
OS	25	28.6±6.5		42	26.7±7.9		12	31.3±8.0	
Chl–NS	65	4.85±1.75	13.46	45	4.89±1.54	9.62	75	5.18±1.78	9.35
OS	25	1.83±0.29		43	2.43±0.75		12	2.67±0.60	

[a]Values significant at the 5% level.

(b) *F*-ratios (regression of corrected Chl) with POC during thermal bar formation in the NS and OS waters of Lake Ontario.

May 1981		
NS	POC = 67.1 Chl + 122.5	$r = 0.85^a$
OS	POC = 80.1 Chl + 14.7	$r = 0.74^a$
May 1982		
NS	POC = 30.7 Chl + 224.9	$r = 0.48^a$
OS	POC = 41.7 Chl + 58.4	$r = 0.76^a$
June 1982		
NS	POC = 57.6 Chl + 133.7	$r = 0.79^a$
OS	POC = 15.3 Chl + 135.1	$r = 0.36$

[a]Value significant at the 5% level.

inputs are usually in excess of autochthonous production and the former are restricted to the nearshore when the thermal bar is in evidence.

Stratification

The thermal bar had dissipated by mid- to late June, and by July, all stations were stratified (stations <20 m in depth were vertically homogeneous at temperatures >4°C). Because Lake Ontario is subject to prevailing westerly winds, upwelling events are common along the northwest nearshore zone (Lee 1972; Gachter et al. 1974; Simons and Schertzer 1987). While such events were observed only during the July cruise of 1981, during 1982, upwelling was evident in July and August and even impacted on the September cruise (see Simons and

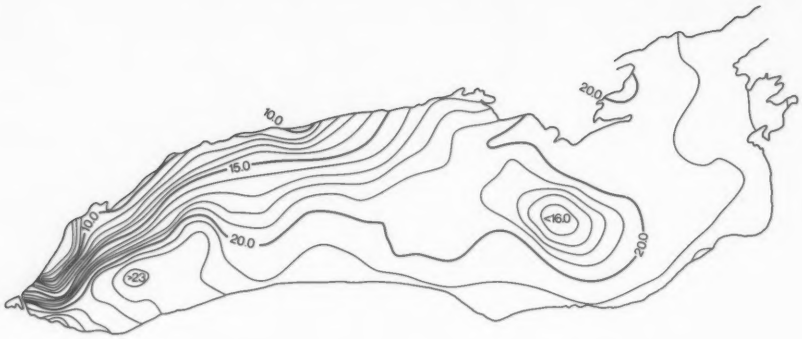

FIG. 4. Surface temperatures (°C) during an upwelling event (August 1982).

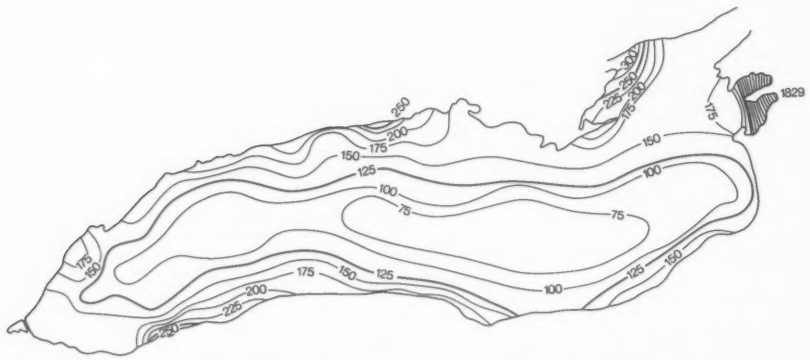

FIG. 5. Summer surface distributions of SRS ($\mu g \cdot L^{-1}$) (August 1981).

Schertzer 1987). During these occurrences, surface isotherms tend to run in an east–northeast to west–southwest direction, unrelated to depth contours. This was particularly evident during August 1982 when surface temperatures in the western nearshore between Toronto and Hamilton declined to 6°C, compared with 20–21°C in the eastern basin (Fig. 4). By mid-September 1982, upwelling effects were diminished and surface temperatures along the northwest ranged from 12 to 15°C.

When PCA was applied to surface data from this cruise, COND, ALK, NO_3, and TFN scored highly on the first factor with TEMP, indicating that the major factor accounting for variability in their surface distributions was upwelling. POC, TPN, CHLA, and TP, loading highly on the second factor, displayed elevated concentrations in the western nearshore and demonstrated a south-to-north increasing gradient. NH_3 and SRS also demonstrated maximum concentrations in the Toronto–Hamilton–Niagara region (15.5 and 198 $\mu g \cdot L^{-1}$, respectively), but elevated levels were also seen in the Kingston Basin; hence, they loaded on a separate factor. SRP, on factor 4, demonstrated little variability lakewide, with concentrations generally <1 $\mu g \cdot L^{-1}$. The Kingston Basin continued to demonstrate lowest surface concentrations (0.70 $\mu g \cdot L^{-1}$) and was the only region of the lake that did not demonstrate a summer decline in SRP, presumably because spring concentrations were already so low (0.83 $\mu g \cdot L^{-1}$).

During the summer full-chemistry cruise of 1981 (August), winds were from the southwest, and there was no evidence of upwelling. Factors resulting from PCA of these data were considerably more difficult to interpret, with only subtle differences being responsible for separation of the variables among the factors. POC, TPN, and CHLA separated out on factor 1, their distributions demonstrating a decreasing concentration gradient from the south shore to midlake, with localized elevated concentrations near the major tributaries (Niagara, Black, Oswego, Genesee, and Welland rivers) as well as Toronto and Hamilton. The nitrogen compounds (NO_3, TFN, NH_3), which scored highly on factor 2, similarly displayed elevated concentrations offshore of the tributaries and urban centres, but also showed extreme concentrations along the western and/or southern shores. NO_3 concentrations in the western nearshore region and along the southern shore between the Niagara and Genesee rivers were two to three times higher than offshore levels. NH_3 demonstrated maximum concentrations in the Toronto–Hamilton–Niagara region, where the area-weighted mean concentration was 24.9 $\mu g \cdot L^{-1}$ compared with 5.2 $\mu g \cdot L^{-1}$ midlake; however, similar low concentrations were observed along the south shore. Ammonia from fertilizers undergoes nitrification in the soil in warm weather. Consequently, agricultural runoff, which contributed ammonia to the southern nearshore in the spring, contributed nitrate in the summer.

Phosphorus variables (SRP, TFP, TP), loading on factor 3, did not exhibit any pronounced nearshore/offshore gradient; however, elevated levels were seen near urban centres and off the major tributaries except the Niagara River. SRS, separating

TABLE 5. PCA of fall chemistry data including POC, TPN, and CHLA.

	16/11/81–20/11/81				15/11/82–19/11/82		
	Factor 1	Factor 2	Factor 3	Factor 4	Factor 1	Factor 2	Factor 3
Eigenvalue	4.08	3.79	2.05	1.41	5.44	2.46	1.86
% var. exp.	31.4	29.1	15.8	10.9	41.9	18.9	14.3
Loadings							
TEMP	−0.04	−0.10	−0.85	0.16	0.29	−0.89	−0.02
COND	−0.10	−0.17	0.58	0.75	−0.31	0.61	−0.21
ALK	−0.02	−0.14	−0.03	0.96	0.12	0.61	−0.07
TP	0.44	0.79	−0.02	−0.19	0.78	−0.61	0.50
SRP	−0.34	0.73	0.37	−0.24	−0.12	0.07	0.91
TFP	−0.02	0.83	0.19	−0.30	0.14	−0.10	0.86
NH_3	−0.03	0.86	−0.21	−0.05	0.51	−0.23	0.26
NO_3	−0.18	−0.12	0.85	0.06	−0.45	0.84	−0.03
TFN	−0.26	0.17	0.86	0.01	−0.36	0.78	−0.04
SRS	−0.09	0.33	0.28	−0.87	0.12	0.74	0.43
POC	0.94	0.19	−0.14	−0.07	0.95	−0.10	0.01
TPN	0.96	0.05	−0.21	−0.02	0.94	−0.22	−0.01
CHLA	0.91	−0.25	−0.04	0.09	0.90	−0.07	−0.20

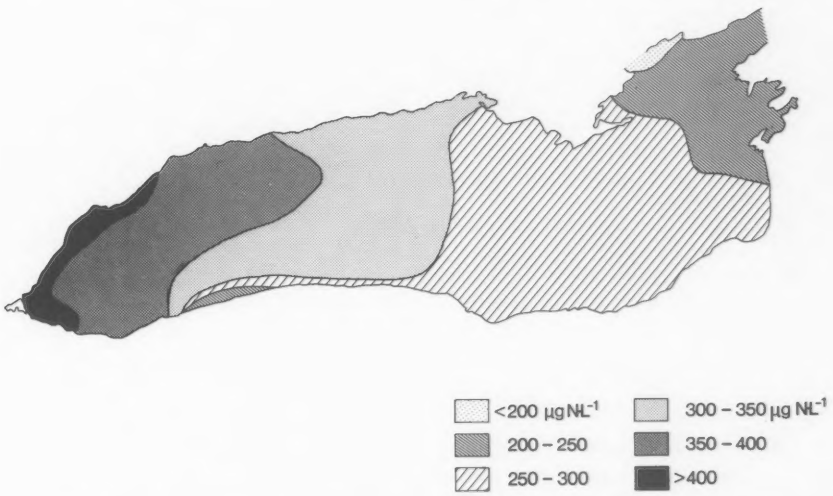

FIG. 6. West-to-east decreasing concentration gradient in fall surface NO_3 (November 1982).

on factor 4, demonstrated minimum levels midlake (60–90 $\mu g \cdot L^{-1}$) compared with the nearshore zone (160–200 $\mu g \cdot L^{-1}$) where tributary inputs were an important factor (Fig. 5).

Loss of stratification

Loss of stratification, and subsequent entrainment of metalimnetic and hypolimnetic waters, generally occurs from northwest to southeast during the fall turnover period (October–December). The range of surface temperatures associated with this differential loss of stratification is substantial, often exceeding 10°C. The surface waters of the deepest area of the lake were the most resistant to breakdown in stratification, raising speculation that the anticyclonic circulation pattern of the lake was maintaining this central gyre, similar to that observed in Lake Huron (Stevens et al. 1985).

As would be expected, those variables that demonstrated significant enrichment in the hypolimnion during the summer stratified period showed elevated surface concentrations in the fall, their distributions reflecting mixing depth (as indicated by temperature). Consequently, the northwest region of the lake exhibited elevated concentrations of NO_3, COND, SRP, and SRS, relative to the southeast regions.

As was observed during the spring and summer, fall (October–December) TP distributions continued to be a function of tributary loadings, with TP concentrations approaching 25–30 $\mu g \cdot L^{-1}$ in the nearshore regions proximate to these sources, relative to midlake concentrations of 10–12 $\mu g \cdot L^{-1}$. The distribution of NH_3 during November was also similar to that observed in spring. Surface area-weighted mean midlake concentrations were 6–8 $\mu g \cdot L^{-1}$, while along the south shore and off tributaries the concentrations were 20–30 $\mu g \cdot L^{-1}$, with maximum values of 55 $\mu g \cdot L^{-1}$ near Toronto.

PCA of fall chemistry data produced three factors (Table 5). The first factor, on which temperature loaded in contrast with

NO_3, TFN, and COND, reflected the northwest–southeast concentration gradient (Fig. 6) which, as discussed, resulted from differential turnover rate. TP and NH_3, loading highly on a second factor, were those variables most affected by nearshore inputs. Fall surface SRS concentrations, affected both by resurgence of hypolimnetic waters and nearshore inputs, separated on the third factor. Inclusion of POC, TPN, and CHLA in the PCA suggested that during November of 1982, distribution of these variables was most affected by nearshore inputs (similar to TP and NH_3); however, during November 1981, POC, TPN, and CHLA distributions were unrelated to any other variables.

In an attempt to discern what factors were controlling distributions of algal biomass in the fall, POC, TPN, and CHLA were regressed against surface temperature. This analysis revealed a complex, but consistent, progression of events. During October of 1981 and 1982, when surface temperatures ranged from approximately 4 to 17°C, POC, TPN, and CHLA exhibited a highly significant positive correlation with temperature. During November of 1981 and 1982, a curvilinear relationship with temperature was observed, where there was a significant positive correlation in the temperature range of 4–7°C and a significant negative correlation between 7 and 10°C. By December 1981, POC, TPN, and CHLA all exhibited significant ($p < 0.05$) negative correlations with temperature. Algal populations in Lake Ontario (excluding the Kingston Basin) are dominated by cryptophytes in October and exhibit sharp declines in abundance when temperatures drop to 6–10°C (Johannsson et al. 1985; Gray 1987). By November, cryptophyte biomass shows marked reduction, with diatoms assuming a greater proportion of the total biomass. However, neither group appears well adapted to the transitional temperatures exhibited during this period. By December, diatoms comprise a large proportion of the algal biomass and appear able to proliferate in regions typified by decreasing temperatures and increasing mixing depth. Thus, the distribution of POM during fall turnover appears to be more responsive to species composition, and its sensitivity to temperature, than to nutrient chemistry.

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Phosphate Ion Interactions at the Sediment–Water Interface in Lake Ontario: Relationship to Sediment Adsorption Capacities[1]

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Manning, P. G. 1987. Phosphate ion interactions at the sediment–water interface in Lake Ontario: relationship to sediment adsorption capacities. Can. J. Fish. Aquat. Sci. 44: 2204–2211.

The chemical forms of iron and phosphorus in surficial sediments of the Niagara Basin of Lake Ontario were determined by Mossbauer spectral and chemical extraction methods. The core locations lie on a transect across a boundary separating sediments displaying a crusty iron- and phosphorus-rich red layer a few centimetres beneath the sediment–water interface from sediments displaying no such layer. Concentrations of nonapatite inorganic phosphorus are relatively low at the surfaces of the layered cores whereas the iron forms are quantitatively similar. It is proposed that the red layers prevent upward diffusion of pore-water ferrous and phosphate ions to the surface. The degree of phosphorus recycling within the top few centimetres of sediment can then be estimated. Approximately 0.035% nonapatite inorganic phosphorus is carried into the anoxic zone. The data, combined with loadings of fine-grained sediment, indicate that Lake Ontario sediments have a net annual binding capacity of ~3500 metric tons of phosphorus, which compares with current loadings of ~8900 metric tons. This binding capacity supports current recommended phosphorus loadings to Lake Ontario.

Les formes chimiques du fer et du phosphore dans les sédiments superficiels du bassin du Niagara du lac Ontario ont été dosées par des méthodes d'extraction chimiques et spectrales de Mossbauer. Les sites de carottage sont situés de part et d'autre de la limite séparant les sédiments ayant une croûte rouge riche en fer et en phosphore, à quelques centimètres sous l'interface sédiments–eau, et les sédiments n'ayant pas de telles couches. Les concentration «d'hydroxydes ferriques» superficielles dont on peut mesurer le E_h sont semblables dans les deux types de carottes, les carottes stratifiées et les carottes non stratifiées; il y a cependant un contraste marqué en ce qui a trait aux concentrations superficielles de phosphore inorganique autre que l'apatite relativement faibles dans les carottes stratifiées. On suppose que les couches ferrugineuses empêchent la diffusion jusqu'à la surface des ions fer et phosphate par l'eau de porosité. La réduction des «hydroxydes ferriques» bruns amorphes dont on peut mesurer le Eh sur la face inférieure de la couche superficielle oxydée entraîne la libération et la diffusion vers le haut des ions fer et phosphate qui réintègrent la couche où ces ions sont précipités. Ainsi, ces «hydroxydes ferriques» sont des liants relativement peu efficaces de l'ion phosphate fraîchement déposé. Ces données, combinées à celles des charges de sédiment finement granulé, indiquent que les sédiments du lac Ontario ont une capacité de rétention annuelle nette d'environ 3500 tonnes de phosphore. Cette capacité permet donc au lac Ontario de recevoir les charges annuelles recommandées de phosphore actuellement déversées dans le lac Ontario.

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Phosphorus is the limiting nutrient in the Great Lakes (Vollenweider 1968; Edmondson 1969; Imboden 1974). Anthropogenic inputs of phosphorus in recent decades have caused marked deterioration in water quality, manifested, for example, in the fouling of beaches by masses of decomposing algae. Controls on phosphorus inputs to Lakes Ontario and Erie, instituted in the early 1970s, have resulted in lower phosphorus concentrations and in increased abundances of oligotrophic algal indicator species (Great Lakes Water Quality Board 1981). Annual target inputs of 7000 metric tons (t) and 11 000 t were determined for Lakes Ontario and Erie, respectively, based on the models of Vollenweider (1976) and Chapra (1978), in which the main indicator parameter was the total phosphorus concentration (10 $\mu g \cdot L^{-1}$ corresponded to a load of ~7000 t annually). The amount of phosphorus deposited annually to the sediments could only be roughly estimated. The phosphorus loading to Lake Ontario in 1982 was 8900 t (Great Lakes Water Quality Board 1983).

Sediments are important sinks for phosphorus, thus reducing the bioavailability of phosphorus to aquatic plants. An estimation of the annual binding capacity of sediments for phosphorus, based on a quantitative understanding of iron–phosphate ionic

[1]Contribution No. 85, National Water Research Institute.

interactions at the sediment–water interface, would provide an important tool for critical assessment of the above target loads. The chemistry of phosphate ion in Great Lakes sediments is strongly controlled by that of iron, and particularly by that of amorphous hydrated ferric oxides (Williams et al. 1976a, 1976b; Manning et al. 1984). Ferric iron and phosphate concentrations are elevated in oxic surficial muds, reflecting the precipitation of E_h-sensitive brown amorphous "ferric hydroxides" (Manning and Jones 1982); these "hydroxides" are efficient substrates for the adsorption of phosphate ion. However, the relative proportions of phosphorus in the oxidized surface layer, derived from pore-water diffusion and from fresh deposition, are not known.

This article reports on the results of Mossbauer spectral and chemical extraction studies of fine-grained sediments retrieved from the Niagara Basin of Lake Ontario. Coring was located on both sides of a boundary separating sediments which display iron- and phosphorus-rich crusty red layers a few centimetres beneath the brown sediment–water interface (Fig. 1) (Sly and Thomas 1974; Manning et al. 1985) from sediments which display no such layer. The aims are (a) to better define forms and concentrations of amorphous or poorly crystalline ferric–phosphate compounds in the sediments, (b) to estimate the relative contributions of pore-water and of freshly deposited phosphate ions to the surface layer, and (c) using these data and fine-grained sediment loadings to Lake Ontario to determine the annual sediment binding capacity for phosphorus.

Methods

Mossbauer (Nuclear Gamma Resonance) Spectroscopy

Mossbauer spectroscopy is based on recoil-free emission and absorption of radiation (Bancroft 1973). A gamma ray emitted by an artificially produced radioactive ^{57}Fe nucleus will be absorbed by a naturally occurring stable ^{57}FE atom, provided both source and target atoms are located in solids. The ^{57}Fe nuclear energy levels are dependent upon the anionic environment. Consequently, to achieve resonant absorption, the source ^{57}Fe is vibrated on a transducer, producing a Doppler velocity shift. Paramagnetic compounds yield spectral doublets, the peak separation being the quadrupole splitting. The shift in the centre of gravity of the doublet, relative to that of a defined absorber (usually iron foil), is the isomer shift. Magnetic iron compounds produce six-line patterns. The spectra of ferrous ions are often diagnostic of the parent compound. However, the spectra of ferric ions in different oxygen environments are often indistinguishable, the superimposition of absorptions producing broadened doublets. The area beneath a given doublet is proportional to ionic abundance.

Experimental Details

One-metre-long Benthos gravity cores were retrieved from 12 locations in the Niagara Basin (Table 1). Cores 1–4 lie on a transect across the western boundary of the ~10 × 10 km area of the Niagara Basin in which crusty red layers occur a few centimetres beneath the sediment surface (Fig. 1). The cores were extruded and sectioned under nitrogen at 1-cm intervals down to 20 cm and at ~5-cm intervals thereafter. The sections were frozen immediately and later freeze-dried. Bottled residuals were stored at −20°C. All cores displayed a 1- to 2-cm-thick brown oxidized surface layer overlying grey muds. Central portions of the cores were selected to eliminate shearing effects along the core-liner walls.

TABLE 1. Information on sediment cores.

Core No.	Date	Location	Depth of water (m)	Depth of red layer (cm)
1	14 Oct. 81	43°20′00″N, 79°30′00″W	90	No layer
2	28 Sept. 83	43°20′00″N, 79°28′00″W	91	No layer
3	28 Sept. 83	43°20′00″N, 79°26′00″W	93	No layer
4	28 Sept. 83	43°20′00″N, 79°24′00″W	95	6–7
5	26 Oct. 82	43°24′00″N, 79°20′00″W	106	4–5
6	7 July 82	43°22′30″N, 79°20′00″W	99	7–8
7	7 Aug. 83	43°22′30″N, 79°20′00″W	99	5–6
8	27 July 82	43°18′06″N, 79°20′00″W	85	17–18[a]
9	23 July 81	43°21′03″N, 79°20′10″W	100	5–6
10	27 Sept. 82	43°16′22″N, 79°20′17″W	85	9–10
11	27 Sept. 82	43°16′21″N, 79°20′48″W	85	9–10
12	18 Nov. 80	43°24′06″N, 79°26′40″W	110	No layer

[a]Brown sandy foreign, possibly dredge, sediment occupies the 9- to 17-cm portion. Cores 1–5 are examined in detail by Mossbauer spectroscopy. Data for cores 8 and 9 were reported earlier by Manning et al. (1985).

Mossbauer spectra were recorded mostly at the National Water Research Institute using a microprocessor-based spectrometer (Cryophysics Ltd., MS103). Some spectra were recorded at McMaster University. Computation of spectra was based on equality of peak half-widths and of peak areas within a quadrupole doublet. Chi-squared values and visual examination of computed fits to the whole spectrum were used as criteria of goodness of fit. The spectrometer was calibrated against iron foil.

Concentrations of nonapatite inorganic phosphorus (NAIP) and of organic phosphorus were measured according to Williams et al. (1976a). Concentrations of total iron and total manganese were measured by bomb digestion and atomic absorption spectrometry (Agemian and Chau 1975). All concentrations are expressed as weight percent of dry sediment.

Particle size analysis yielded 0% sand, 30–55% clay, and 70–45% silt for red layer and unlayered sediment. ^{210}Pb dating has shown that the red layers in cores 5–8 are overlaid by ~65 yr of continuous deposition (Manning et al. 1985).

Results and Discussion

Mossbauer Spectra and Forms of Iron

All spectra are qualitatively similar to that in Fig. 2 and all can be adequately computer fitted assuming the presence of two doublets (Coey et al. 1974; Manning and Jones 1982). The outer doublet has Mossbauer parameters (IS = isomer shift = 1.13 mm·s^{-1}, QS = quadrupole splitting = 2.61 mm·s^{-1}, and HW = half-width = 0.41 mm·s^{-1}) consistent with ferrous ions in the lattice of chlorite (Bancroft 1973). Chlorite was confirmed by X-ray diffraction analysis. The inner broadened doublet (correspondingly, 0.37, 0.65, and 0.57 mm·s^{-1}) marks ferric ions in a range of anionic environments, principally amorphous or poorly crystallized hydrated ferric oxides (Coey et al. 1974; Manning and Jones 1982). All parameters are precise to ±0.02 mm·s^{-1}. The ferric iron absorption contains contributions from brown E_h-sensitive ferric iron (E_hFE^{3+}, restricted to the brown oxidized surface layer) and from more

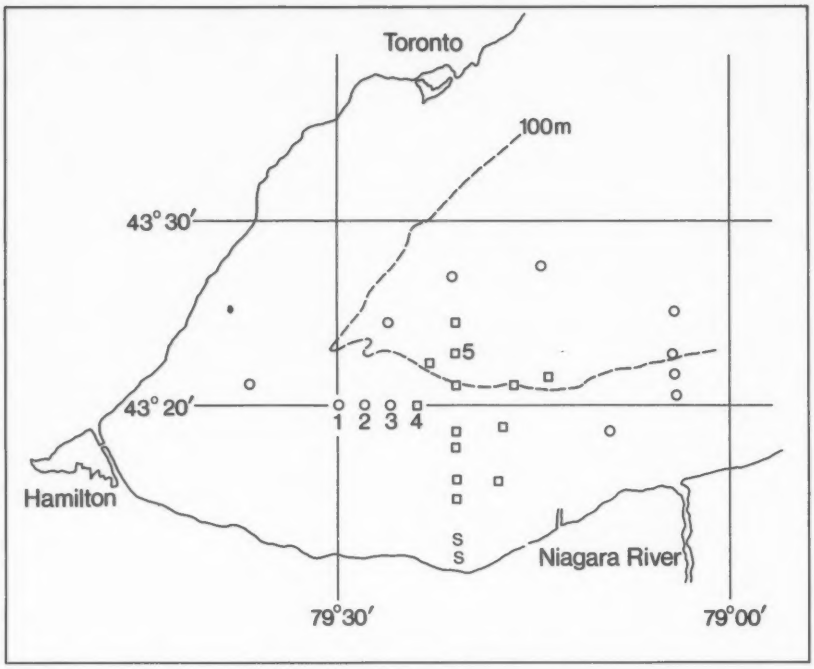

FIG. 1. Locations of cores 1–5 in the Niagara Basin. Squares mark red layer cores, circles mark nonlayered cores, and S represents sand.

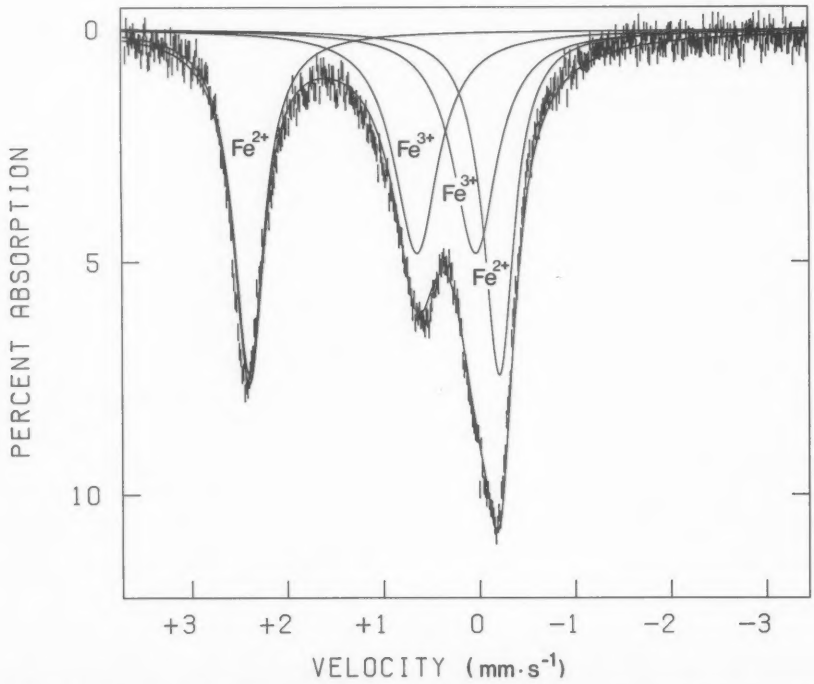

FIG. 2. Representative room-temperature Mossbauer spectrum of Niagara Basin mud showing computed fit based on two doublets. Chi-squared is 750 for 500 degrees of freedom.

TABLE 2. Concentrations (wt. %) of F^{3+} (normalized) against sediment depth. Total iron concentrations in the top 1 cm are listed in Table 5. All cores contain 6% of total iron in hematite. For core 6, Fe^{3+} is 3.02% at 0–1 cm, 2.56% at 3.4 cm, and 2.09% at 4–5 cm; for core 7, Fe^{3+} is 2.08% at 0.1 cm and 1.68% at 2–3 cm (normalized values).

Depth (cm)	Core 1	Core 2			Core 3,	Core 4			Core 5,
	Fe^{3+}_{norm}	Fe^{2+}	Fe^{3+}	Fe^{3+}_{norm}	Fe^{3+}_{norm}	Fe^{2+}	Fe^{3+}	Fe^{3+}_{norm}	Fe^{3+}_{norm}
0–1	1.96	1.435	1.90	1.90	1.91	1.316	1.85	1.85	2.00
1–2	1.87	1.453	1.66	1.64	1.63				1.69
2–3	1.49	1.751	1.70	1.39	1.37	1.756		1.34	1.52
3–4	1.25	1.793	1.74	1.39[a]	1.36	1.651		1.30	1.48
4–5	1.31	2.115	1.985	1.35	1.24	1.982		1.25	10.6 (RL)
5–6		1.749	1.70	1.40	1.32			10.5 (RL)	
6–7	1.37	1.831	1.74	1.36					1.19
7–8		1.706	1.86	1.57		2.060	1.72	1.10	1.22
8–9		1.955	1.62	1.19	1.53				
9–10	1.36	2.039	1.80	1.27		2.045	1.42	0.91	1.29
10–11	1.25	1.747	1.73	1.42	1.10	1.904	1.60	1.10	
11–12	1.53	1.749	1.73	1.42	1.11				1.15
12–13	1.14	1.855	1.63	1.26	1.22				1.55
13–14	1.19	1.915	1.38	1.03	1.61				0.95
14–15					1.36				1.41
18–19						2.009	1.49	0.98	1.06
21–22		2.007	1.28	0.92					
22–23		1.675	1.62	1.38					
29–30						2.182	1.50	0.90	

[a]For example, $Fe^{3+}_{norm} = 1.74\% \times (1.435/1.793) = 1.39\%$.

TABLE 3. Concentrations of carbon forms in core 2 (n.m. = not measured).

Depth (cm)	Total C	Organic C	CH_2O[a]	Inorganic C	$CaCO_3$[b]	Norm factor (Mossbauer)
0–1	5.71	4.13	10.33	1.58	13.16	1.00
3–4	3.95	3.36	8.40	0.59	4.91	0.80
6–7	2.68	2.58	6.45	0.10	0.83	0.78
7–8	2.42	2.34	5.85	0.08	0.67	0.84
8–9	2.22	2.25	5.63			0.73
9–10	2.14	2.15	5.38			0.70
11–12	1.97	1.97	4.93			0.82
12–13	1.83	1.75	4.38			0.77
13–14	1.76	1.74	4.35			0.75
16–17	1.57	1.57	3.93			n.m.
18–19	1.69	1.68	4.20			n.m.

[a]Assumed average composition of organic matter.

[b]Based on all inorganic carbon being in $CaCO_3$. Total carbon was measured by combustion in a Leco induction furnace and organic carbon by dry combustion after removal of carbonate by acid.

E_h-resistant compounds, e.g. hydrated oxides, ferric ions in clay lattices, and in amorphous ferric aluminosilicates formed surficially (Nriagu 1978; Manning and Jones 1982). For convenience, the latter group has been termed refractory ferric compounds (RFCs). RFCs are slowly reduced in Great Lakes sediments (Manning et al. 1984) but rapidly in sulfide-rich sediments (Manning et al. 1979). Measured concentrations of ferrous and ferric ions (Table 2) are consistent for cores 1–5 over the top 6–7 cm of sediment. Concentrations of ferrous ions increase with increasing depth of burial (cores 2 and 4, Table 2), reflecting the loss of calcium and magnesium carbonates and of organic matter on burial (Table 3) (Kemp and Thomas 1976; Kemp et al. 1976; Manning and Jones 1982). Using ferrous ions in chlorite as a conservative indicator (Manning and Jones 1982; Kemp and Thomas 1976), ferric ion concentrations have been normalized against the ferrous ion concentration in the top 1 cm of each core (Table 2). Normalization corrects for the minor changes which have occurred since colonial settlement (Kemp et al. 1976).

The room-temperature Mossbauer spectra of the red subsurface layers in cores 4 and 5 are dominated by the broad ferric doublet, reflecting the precipitation of ferric oxides (Manning et al. 1985). Calculated Mossbauer parameters for cores 4 and 5 are as follows: FE^{2+}, IS = 1.13 mm·s^{-1}, QS = 2.61 mm·s^{-1}, and HW = 0.42 mm·s^{-1}; Fe^{3+}, IS = 0.38 mm·s^{-1}, QS = 0.76 mm·s^{-1}, and HW = 0.54 mm·s^{-1}. The large QS value for ferric ion is consistent with the presence of ferrihydrite ($5Fe_2O_3 \cdot 9H_2O$), which is formed when ferrous-rich percolating groundwaters meet an oxygen-rich environment (Coey and Readman 1973; Murad and Schwertmann 1980; Manning et al. 1985). In Lake Ontario sediments, ferrihydrite may have crystallized at the sediment–water interface during a period of low sedimentation rate (Manning et al. 1985).

Spectra recorded over the range −9 to +9 mm·s^{-1} display the outer peaks of detrital hematite, α-Fe_2O_3 (Manning et al. 1984, 1985). Computation shows that ~6% of total iron is in hematite. Its role in binding phosphate ion is probably negligible.

Estimation of E_hFE^{3+} Concentrations

Plots of normalized ferric iron concentrations against sediment depth (i.e. time) for Niagara Basin cores 1–4 are remarkably similar over the top 6–7 cm of sediment (Fig. 3), showing the marked enhancement in surficial (top 1 or 2 cm) ferric iron that is characteristic of cores with prominent oxidized

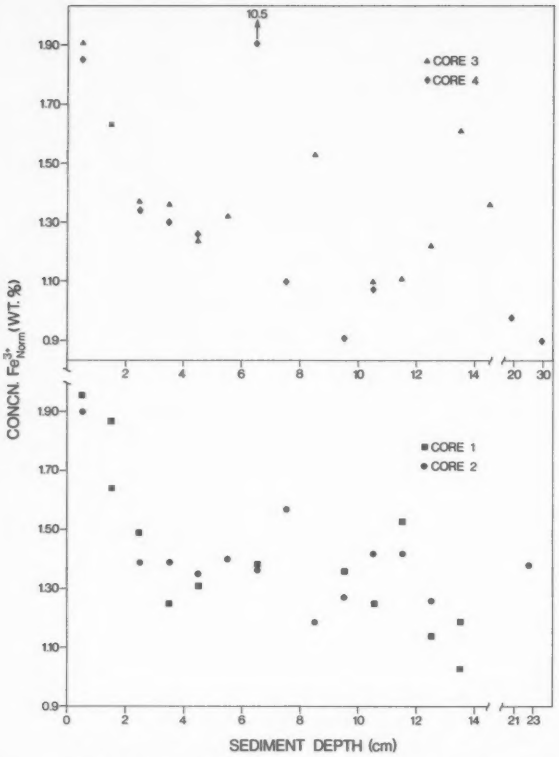

FIG. 3. Plots of normalized ferric iron concentrations against depth beneath the sediment–water interface for cores 1–4.

surface layers (Manning et al. 1984). Beneath 7 cm, however, the plots of all cores display considerable scatter in ferric iron concentrations to a degree not previously observed in Great Lakes sediments (Manning et al. 1984; Manning and Jones 1982). The cause of this scatter may be related to the formation of the red layers, i.e. to possible changes in sedimentation patterns (Manning et al. 1985). Assuming a first-order process for the decay of RFCs (Manning and Jones 1982; Manning et al. 1984), concentrations of RFCs in the oxidized surface layer can be estimated by extrapolating the best straight line (linear least squares regression) in a log $[Fe^{3+}_{norm}]$ against depth plot, through points in the anoxic zone to the oxic–anoxic boundary, i.e. to the underside of the oxidized surface layer. The large scatter for points beneath 6–7 cm makes the regression analysis impracticable for each curve. However, concentrations of RFCs and E_hFe^{3+} in the oxidized surface layer can be calculated as follows. The averaging of RFC concentrations over the range 2–3 cm through 6–7 cm for cores 1–4 ($=1.34 \pm 0.05\%$ FE^{3+}) and the subtraction of this value from the average total ferric concentration in the top 1 cm for the four cores ($=1.91 \pm 0.05\%$ Fe^{3+}) yields an E_hFE^{3+} value of $0.57 \pm 0.1\%$ Fe^{3+}. This value is in good agreement with those measured for other Lake Ontario cores (Manning et al. 1984) and for core 5 (Tables 2 and 4). The error involved in the calculation is small because of the weak dependence of RFC concentration on sediment depth for well-oxidized Lake Ontario cores (Manning et al. 1984). Clearly, differences in the forms and concentrations of iron compounds at the surfaces of cores 1–4 are insignificant.

TABLE 4. Concentrations of iron, manganese, and phosphorus forms in the top 1 cm of cores. The RFC concentration is equal to the concentration of Fe^{3+} (normalized) at the underside of the oxidized surface layer. n.m. = not measured. Cores 4–11 have red layers.

Core	Total Fe	Fe^{2+}	RFC	Total Mn	E_hFe^{3+}	NAIP
1	3.43	1.26	1.34	0.76	0.57	0.144
2	3.55	1.44	1.34	0.77	0.57	0.090
3	3.48	1.36	1.34	1.08	0.57	0.062
4	3.37	1.32	1.34	0.74	0.57	0.048
5	3.80	1.57	1.50	0.61	0.50	0.051
6	4.90	1.77		1.08	Table 2	0.047
7	3.55	1.42		n.m.	Table 2	0.046
8	3.81	1.47	1.41	0.63	0.65	0.068
9	6.62	2.43	2.74	0.63	0.58	0.069
10	3.31	n.m.		0.27	n.m.	0.045
11	3.31	n.m.		n.m.	n.m.	0.034
12	4.28	1.99	1.75	0.65	0.54	0.083

Moreover, redox potentials and organic carbon values at the surfaces of several of the cores show no obvious trends (Table 5).

Forms of Manganese

Concentrations of total manganese are strongly elevated at the surfaces of the three nonlayered cores and five of six red layered cores (Table 5): background concentrations of ~0.1% manganese are attained in almost all cores by ~5 cm burial. This surficial enhancement reflects the precipitation of oxidized manganese ions under conditions of high redox potential (Kemp and Thomas 1976). Ferric ions are precipitated at lower redox potentials than are maganese ions, and relatively high E_hFe^{3+} values are to be expected for red layer cores 4,5,8, and 9 (Manning et al. 1985). The relatively small elevation in surficial manganese concentrations in core 10 reflects a slightly lower redox potential, but one, nevertheless, that is sufficiently high to precipitate ferric iron.

Ferric–Phosphate Ionic Interactions

Cores 1–5 and core 12 display consistently high concentrations of E_hFe^{3+} (Tables 4 and 5); high concentrations of E_hFe^{3+} can also be inferred from the partial data for cores 6 and 7 (Table 2). From the relationship derived earlier (Manning et al. 1984), i.e. $[NAIP] = 0.035 + 0.08\ [E_hFe^{3+}]$, where [ ]01 represents concentrations in weight percent and where 0.035% is the concentration of RFC-adsorbed phosphorus, expected NAIP concentrations in the oxidized surface layers of the current cores are ~0.08%. Core 2 clearly satisfies this condition (Tables 4 and 6); the relatively high value for core 1 may reflect precipitation of crystalline ferric phosphates (Berner 1973). However, six of the eight red layer cores have surficial NAIP concentrations of 0.051% or less, and, significantly, NAIP concentrations decrease progressively from core 1 through core 4 (Tables 4 and 6). Low NAIP concentrations are therefore a feature of surface muds over most of the red layer region. Because the iron chemistry, redox potentials, and differences in organic matter deposition (Table 5) can be eliminated as the cause of the low NAIP values (Tables 4 and 6), then the red layers are effective barriers to the upward diffusion of pore-water phosphorus. The marked contrast between NAIP concentrations within the red layers and in the 1 cm of mud above suggests minor leakage of

TABLE 5. Concentrations of manganese and organic carbon (wt. %) in sections of freeze-dried sediment cores. meas = measured norm; norm = normalized (against Fe^{2+} in chlorite). Depths >18 cm are 62–63 cm (core 2), 29–30 cm (core 4), 18–19 cm (core 5), 41–42 cm (core 8), and 83–84 cm (core KB, Kingston Basin). Error in Mn values is ±10%.

	Core 2		Core 3		Core 4		Core 5		Core 8		Core 9		KB,
Depth (cm)	meas	norm	meas	norm	meas	norm	meas	norm	meas	norm	meas	norm	meas
0–1	0.77	0.77	1.08	1.08	0.74	0.74	0.61	0.61	0.63	0.63	0.63	0.63	0.11
1–2	0.34	0.34	0.57	0.51	0.62		0.42	0.39	0.25	0.22	0.32	0.49	
2–3	0.23	0.19	0.29	0.22	0.27	0.20	0.17	0.14	0.17	0.14	0.24	0.58	0.07
3–4					0.24	0.19			0.15	0.12			
4–5	0.21	0.14			0.25	0.17	1.95	1.73[a]			8.41[a]	13.6[a]	
5–6	0.24	0.20	0.40	0.27	1.61[a]								
6–7									0.10	0.07			
7–8			0.21	0.15	0.20	0.13	0.10	0.08					
8–9									0.10	0.07			
9–10	0.22	0.15	0.22	0.16	0.14	0.09					0.08	0.19	0.06
11–12							0.12	0.09					
>18	0.18	0.16			0.09	0.05	0.07	0.05	0.09	0.06			
Organic C (0–1)	4.13				4.67						4.7		0.08
E_h (mV) (0–1)	+300		+320		+320				+350				+25 060

[a]Represents red layer.

TABLE 6. Normalized concentrations (wt. %) of NAIP against sediment depth. Estimates error in NAIP values is ±5%.

Depth (cm)	Core 1	Core 2	Core 3	Core 4	Core 5	Core 6	Core 7	Core 8	Core 9	Core 10	Core 11	Core 12
0–1	0.144	0.090	0.062	0.048	0.051	0.047	0.046	0.068	0.069	0.045	0.034	0.083
1–2	0.086	0.086	0.066	0.052	0.053		0.055	0.074		0.041	0.016	0.065
2–3		0.068	0.036	0.033	0.040		0.039		0.047			0.050
3–4		0.047	0.038	0.034	0.031	0.042			0.042			0.051
4–5	0.109	0.056	0.032	0.027	1.83[a]	0.048		0.040				0.035
5–6		0.040	0.040	0.91[a]	0.013		0.68[a]		0.85			0.043
6–7		0.045										0.018
7–8		0.109		0.027		1.64[a]						0.044
8–9		0.025	0.027	0.113		0.027	0.010					
9–10	0.042	0.071		0.013		0.011	0.015					
10–11		0.040	0.015	0.023			0.013					
11–12	0.074	0.027	0.011									
12–13	0.023	0.019				0.013			0.025	0.37[a]		
13–14	0.048	0.019	0.108									
14–15		0.267	0.035									
17–18								0.52[a]		0.006		

[a]Red layer material (cores 4–11). Approx. 9 cm of foreign material covered the red layer in core 8; hence, the greater apparent depth (Manning et al. 1985).

NAIP from the layer (cores 4 and 5, Table 6). The low surficial NAIP values in tbe red layer cores are the sum of external loading to the sediment plus the reduced internal loading since red layer formation (Manning et al. 1985). The internal loading is derived from phosphate ion released on reduction of RFCs and on mineralization of organic phosphorus compounds in the anoxic zone; in nonlayered sediments, however, additional significant internal loading is derived from the reduction of $E_h Fe^{3+}$-P at the underside of the oxidized surface layer. Hence, the external loading of phosphorus to the Niagara Basin sediments supports a maximum 0.05% NAIP in the top 1 cm; moreover, in oxic nonlayered sediments, at least 0.03% NAIP is regenerated internally (0.08% for cores 2 and 12 minus 0.05%). Further, the net sediment binding capacity for NAIP cannot exceed 0.05% phosphorus.

A maximum net sediment binding capacity of 0.05% NAIP is consistent with chemical principles. The surficial enrichment in ferric and phosphate ions (Tables 4 and 6; Fig. 3) reflects the reduction and dissolution of $E_h Fe^{3+}$-P at the oxic–anoxic boundary followed by upward diffusion of the ferrous and phosphate ions back into the oxidized surface layer. The ferric iron profiles (Fig. 3) place the boundary at 1–2 cm depth, coincident with the onset of major decreases in NAIP concentrations (Table 6). Reduction of RFCs is relatively slow beneath the oxic–anoxic boundary (Fig. 3) (Manning and Jones 1982). A proportion of the ferrous and phosphate ions released at the boundary will be precipitated as vivianite, $FE_3(PO_4)_2 \cdot 8H_2O$, which is formed in the anoxic region of Lakes Erie and Ontario sediments (Nriagu and Dell 1974). However, the rapid loss of NAIP beneath the oxidized surface layer (Table 6) indicates that minor amounts of phosphorus are incorporated into vivianite. Hence, most of the ferrous and phosphate ions derived from the reduction of $E_h Fe^{3+}$-P are recycled back into the oxidized surface layer. The amount of NAIP carried into the anoxic zone

TABLE 7. Concentrations (wt. %) of organic phosphorus in Lake Ontario sediments. KB = Kingston Basin; n.m. = not measured; norm = normalized against Fe^{2+}; meas = measured. Three cores from the Kingston Basin (KB) contained 0.067, 0.056, and 0.045% NAIP in the top 1 cm; two cores from the Rochester Basin contained 0.055% NAIP.

Depth (cm)	Core 3		Core 4		Core 5, norm	Core 7, meas	Core 11, meas	Core 12, norm	KB, meas
	meas	norm	meas	norm					
0–1	0.047	0.047	0.050	0.050	0.051	0.042	0.019	0.034	0.059
1–2	0.034	0.030	0.037	0.033	0.038	n.m.	0.010	0.027	0.054
2–3	n.m.	n.m.	n.m.	n.m.	n.m.	0.040	n.m.	0.020	0.044
3–4	n.m.	n.m.	n.m.	n.m.	n.m.	0.035	n.m.	0.020	0.041
4–5	0.029	0.020	0.031	0.021	0.023	0.038	n.m.	0.018	0.037
5–6	n.m.	n.m.	0.027	~0.02	n.m.	0.025	0.020	0.017	n.m.
8–9	0.025	0.018							0.032

is ~0.035% (i.e. RFC-P) (Manning et al. 1984) plus vivianite-P, the sum of which is unlikely to exceed 0.05% phosphorus in well-oxidized nonlayered sediments. In red layer sediments and in low redox sediments, which respectively display low NAIP and low NAIP plus low $E_h Fe^{3+}$ concentrations at the surface, vivianite formation is hindered. Significantly, ~0.035% NAIP is carried into the anoxic zone in red layer cores (Table 6).

The surficial muds in the red layer region are, therefore, undersaturated with respect to adsorbed phosphate ion. The high proportion of NAIP carried to 2–3 cm depth and deeper (cores 4 and 5, Table 6) suggests that most of the NAIP is adsorbed on RFCs because $E_h Fe^{3+}$-P would be remobilized to the oxidized surface layer on reduction at the oxic-anoxic boundary. This undersaturation of $E_h Fe^{3+}$ with respect to phosphate ion is surprising in these times of excessive fertilization and eutrophication. Most of the fine-grained sediment introduced to Lake Ontario by the Niagara River is carried immediately eastward along the south shore and is deposited in the eastern Rochester and Kingston basins (Kemp and Harper 1976) in which sedimentation rates are relatively high and redox potentials and NAIP values are relatively low (Tables 5 and 7) (Manning et al. 1984; Kemp and Harper 1976).

Significant sediment binding capacity is also contained within the organic phosphorus fraction. Concentrations of organic phosphorus in surficial muds of Lakes Erie and Ontario are in the range 0.02–0.05% (Table 7) (Williams et al. 1976a, 1976b), which values decrease to ~0.025% after ~3 cm burial. The phosphorus released migrates upward, as phosphate ion, to the oxidized surface layer and contributes to internal loading. A net binding capacity of 0.025% organic phosphorus seems reasonable for Niagara Basin muds. For red layer sediments, therefore, the binding capacity for phosphate is 0.035% NAIP plus 0.025% organic phosphorus, or ~0.06% phosphorus; for nonlayered well-oxidized sediments, with higher surficial NAIP concentrations, there is additional binding capacity in vivianite. Hence, an average capacity for Niagara Basin muds is not greater than 0.07% phosphorus.

Binding Capacities of Lake Ontario Sediments

The annual input of fine-grained sediment to Lake Ontario is $\sim 9.1 \times 10^6$ t, half of which enters via the Niagara River (Kemp and Harper 1976). The outflow of fine-grained sediment is $\sim 3.4 \times 10^6$ t, yielding a net deposition to the sediments of $\sim 5.7 \times 10^6$ t annually. Based on average rates of sedimentation, Kemp and Harper (1976) calculated a fine-grained sediment deposition of 4.8×10^6 t annually, with the Niagara (western), Mississauga (middle), Rochester (eastern), and Kingston (far eastern) basins receiving ~16, ~15, ~54, and ~15% of the input, respectively. Averaging the fine-grained sediment loads (5.25×10^6 t annually), the four basins receive, respectively, 0.84×10^6, 0.79×10^6, 2.84×10^6, and 0.79×10^6 t annually. In the absence of significant diagenesis, the compositions of the top 1 cm of depositional sediment and of the fine-grained sediment entering the lake are assumed to be similar. Redox processes in the Niagara and Mississauga basins are probably similar (Manning et al. 1984), both having red-layered and well-oxidized sediments. Hence, the binding capacity of Niagara and Mississauga Basin sediments for phosphorus is $1.63 \times 10^6 \times 0.07 \times 10^{-2}$, or ~1140 t annually.

Surficial sediments of the Rochester and Kingston basins have generally lower concentrations of NAIP and/or $E_h Fe^{3+}$ (Table 7; Manning et al. 1984), reflecting lower redox potentials (Table 5). Oxygen depletion occurs in the bottom waters of the Kingston Basin in summer (Dobson 1967). Ferromanganese nodules, which occur along the north shore, may indicate iron release from the offshore sediments (Damiani et al. 1973). Furthermore, the Kingston Basin is eutrophic (Great Lakes Water Quality Board 1981, 1983), indicating relatively higher deposition of organic matter (Kemp and Thomas 1976). Vivianite will, therefore, make a smaller contribution to the binding capacity. The net binding capacity contained within NAIP and organic phosphorus is probably less than 0.035 plus 0.030%, or 0.065% phosphorus. The fine-grained sediment load is 3.6×10^6 t annually, yielding an annual binding capacity of ~2340 t of phosphorus. For the whole lake, therefore, the binding capacity is ~3500 t of phosphorus annually, which compares with loadings of ~13 700 t in 1968 and 8900 t in 1982; the current target is 7000 t annually (Great Lakes Water Quality Board 1983). The cause of lower water quality and of increased eutrophic indicator species in the 1960s and 1970s is clearly the input of large amounts of weakly bonded (insufficient iron) and weakly sedimented phosphate. Phosphate ion that is not bonded to ferric compounds in fine-grained sediment is more easily released on depletion of soluble phosphate ion depletion in the water, and is therefore readily bioavailable.

The ~3500 t difference between recommended input (7000 t) and the sediment binding capacity (~3500 t) corresponds to an equilibrium phosphorus concentration in the overlying water of ~17 $\mu g \cdot L^{-1}$, which compares favourably with current measured values of ~13 $\mu g \cdot L^{-1}$. This first calculation of sediment binding capacity is clearly approximate, with an estimated error of approximately ±50%. Nevertheless, the calculations do lend

considerable support to current target inputs. Note that even if the sediment binding capacity is underestimated by 50%, the difference between 7000 and ~5000 t would yield an equilibrium phosphorus concentration in the overlying water of ~10 $\mu g \cdot L^{-1}$; this is the value used in the models of Vollenweider (1976) and Chapra (1978).

Other sinks for phosphorus do exist in Lake Ontario in the form of manganese nodules (in the Bay of Quinte and on the north shore of the Kingston Basin) and ferromanganese-coated sands (extensive along the north shore of the Mississauga Basin) (Sly and Thomas 1974; Damiani et al. 1973). The rate of accumulation of iron and phosphorus in these concretions and crusts is not known, and it is conceivable that the nodules are slowly dissolving (Damiani et al. 1973). Neither is likely to be a major sink for phosphorus.

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Reduction of *Cladophora* Biomass and Tissue Phosphorus in Lake Ontario, 1972–83

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Cladophora biomass and tissue phosphorus concentrations at seven sites in Lake Ontario have decreased from 1972 to 1983 in response to phosphorus control programs introduced in the early 1970's. Biomass and tissue phosphorus were significantly different between 1972 and 1982–83 (ANOVA, $P < 0.001$) but not significantly different between 1982 and 1983. The lakewide average tissue phosphorus was 0.49% in 1972 but by 1982 and 1983 had dropped to 0.26 and 0.20%, respectively, on an ash-free dry weight basis. Tissue phosphorus concentrations did not limit growth in 1972 but in 1983 had begun to limit growth. Model-predicted net production for a 6-wk sampling period in 1983 was 1.7 times greater in the western end of the lake than at a remote site in eastern Lake Ontario due to higher soluble reactive phosphorus concentrations.

Les concentrations de phosphore dans les tissus et la biomasse de *Cladophora* à sept endroits dans le Lac Ontario ont diminué de 1972 à 1983 suite aux programmes de lutte contre le phosphore lancés au début des années 70. Les concentrations de phosphore dans les tissus et la biomasse présentent était des écarts significatifs entre 1972 et 1982–83 ANOVA $P < 0{,}001$), mais non significatifs entre 1982 et 1983. La teneur moyenne en phosphore (poids sec sans cendre) des tissus dans tout le lac était de 0,49% en 1972, mais a chuté en 1982 et 1983, à 0,26% et 0,20% respectivement. Les concentrations de phosphore dans les tissus n'ont pas limité la croissance en 1972, mais ont commencé à le faire en 1983. La production nette prévue par modélisation pour une période d'échantillonnage de 6 semaines en 1983 était de 1,7 fois plus élevée à l'extrémité occidentale du lac qu'à un endroit éloigné dans l'est du Lac Ontario, à cause de la présence de fortes concentrations en phosphore réactif soluble.

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Since the mid-1950's, growths of the filamentous alga, *Cladophora*, have created problems along the Lake Ontario shoreline. Large odoriferous masses of decaying *Cladophora* are frequently washed up onto shore by storms during the summer growing season. The decaying *Cladophora* is aesthetically unpleasant, a barrier to recreation, and has been implicated in taste and odor events in drinking water supplies (Brownlee et al. 1984).

Cladophora growth is regulated by a combination of environmental factors including light, temperature, and phosphorus availability (Canale and Auer 1982). *Cladophora* grows attached to rocky substrates, so the extensive bedrock shelf in Lake Ontario from Burlington to Toronto provides an adequate habitat for the accumulation of *Cladophora* biomass. Phosphorus inputs into Lake Ontario have been controlled, and spring soluble reactive phosphorus (SRP) and total phosphorus (TP) levels have dropped 67 and 58% respectively, in the open lake since 1973, approaching the target concentrations in 1983 (Dobson 1985; Stevens and Nielson 1987).

Cladophora biomass and tissue phosphorus were sampled at seven sites in Lake Ontario in 1972 when phosphorus concentrations in Lake Ontario were approaching their maximum. The Ontario Ministry of Environment conducted the survey as part of the International Field Year for the Great Lakes (IFYGL). To determine if the phosphorus control programs have affected the *Cladophora* standing crop or tissue phosphorus concentrations and hence growth, Environment Canada contracted Limnos Ltd. to repeat one of the three sample series conducted in 1972 in 1982 and conduct three sample series in 1983. Water quality data was also collected to model the current growth potential of *Cladophora* in Lake Ontario.

Methods

The seven sites chosen in 1972 were Oakville, Whitby, Cobourg, Presqu'ile, Point Petre, Bath, and Emeric Point (see Fig. 4). The 1972 stations were sampled on three occasions, June 4–6, July 5–12, and August 5–10. The 1982 survey was performed on July 6–14 at the seven sites to determine if significant changes had occurred over the 10-yr period. Based on the 1982 survey, a decision was made to survey on three occasions in 1983 but to change the sampling times to June 8–15, June 21–29, and July 5–13 with the hope of recording the seasonal peak biomass. Sampling was not conducted in August 1983 because the lake is normally too warm and the *Cladophora* beds have died and sloughed off by August. Thus, one survey in

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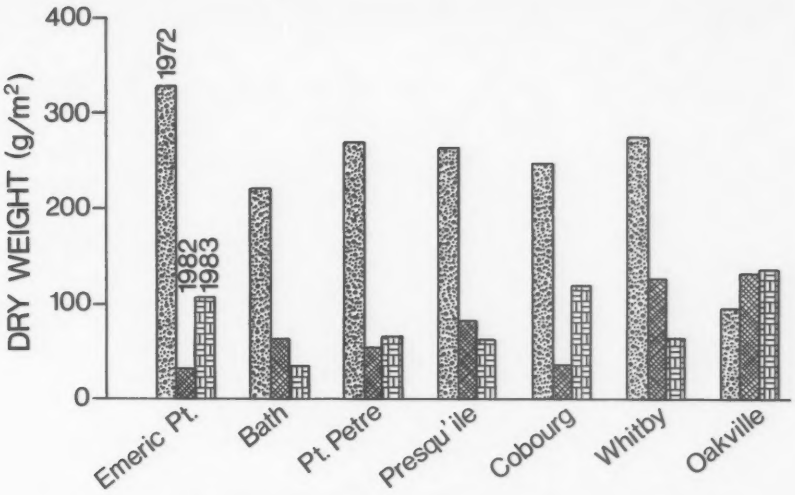

FIG. 1. *Cladophora* biomass in 1972, 1982, and 1983 at each sampling station.

1982 and two surveys in 1983 were directly comparable with the 1972 surveys.

Cladophora was sampled by Scuba at four depths, 0.5, 1.5, 3.0, and 5.0 m at each site. At each depth, three replicate 0.25-m^2 quadrats were cropped by diver and collected on the surface vessel by a gasoline-powered venturi pump (Limnos Ltd. 1981). Collected algae were weighed, their volume measured by displacement, and frozen pending analysis. Biomass samples were analyzed for percentage of dry weight, loss on ignition (LOI), and total tissue phosphorus. The LOI was used to correct the tissue phosphorus concentration to an ash-free dry weight basis (AFDW). The correction to AFDW was necessary to eliminate the differences in ash content in samples from the different years and different depths. The highly productive 1972 *Cladophora* samples had high ash contents compared with the less productive 1982–83 samples. The analyses for phosphorus were conducted by the Ontario Ministry of Environment's Rexdale Laboratory.

Water samples for SRP and TP were taken near the shore at 1.5- and 5.0-m depths and offshore at twice the distance of the 5.0-m site. Water samples for SRP analyses were filtered in the field using acid-rinsed 0.45-μm milllipore filters, stored on ice in the field, and refrigerated until analyzed. Water samples for TP were preserved with 1 mL of 5% sulphuric acid, stored on ice in the field, and refrigerated until analyzed.

Secchi depths and water temperatures measured at the seven sites were used along with the SRP data to predict *Cladophora* tissue phosphorus and net production for the 6-wk period in 1983. The model was modified after Auer and Canale (1982). The predicted tissue phosphorus was compared with the actual tissue phosphorus and the 6-wk net production response was used to compare the stations with one another.

Results and Discussion

With the exception of the Oakville station, all stations showed a substantial reduction in standing crop between 1972 and 1982–83 (Fig. 1). Standing dry weight, averaged over all stations and all depths, was 205.8, 80.0, and 85.9 g/m^2 for 1972, 1982, and 1983, respectively, which is a 58% decrease in biomass between 1972 and 1983. An analysis of variance (ANOVA) of the standing crop AFDW measurements from identical depths, times, and stations indicated that the 1972 data were significantly different from the 1982 and 1983 data ($P < 0.001$). However, the 1982 and 1983 data were not significantly different. No definite geographical trends for biomass along the Lake Ontario shoreline were apparent.

The standing crop of *Cladophora* present at any one time is dependent on the difference between growth rate and the rate of removal. For example, storms can completely scour the bottom, making interpretation of the data difficult. Standing crop estimates must be tempered with an understanding of the factors controlling the quantity observed at any one time. A much more reliable measurement to use for yearly and station to station comparisons is tissue phosphorus.

Seasonal averages of tissue phosphorus (Fig. 2) are expressed on an AFDW basis to correct for seasonal and year to year variations in ash content. At all locations, the 1983 tissue phosphorus levels were less than the 1972 concentrations. The 1972 average tissue phosphorus was 0.49% (AFDW) compared with 0.20% in 1983. This represents a 59% reduction in tissue phosphorus over the 11-yr interval. With the exception of the Presqu'ile site, the 1982 data were comparable with the 1983 levels, with an average of 0.26% phosphorus (AFDW). An ANOVA of the tissue phosphorus data (AFDW) from identical times, depths, and stations indicated that the 1972 data were significantly different from the 1982 and 1983 data ($P < 0.001$). The 1982 data were not 95% significantly different from the 1983 data. The Point Petre shoreline had the lowest tissue phosphorus concentration in 1972 because the site is quite remote and is probably the least eutrophic of the seven sites. The other six sites, although they were not located near any point sources of nutrients, were influenced by their proximity to urban areas. The Point Petre *Cladophora* tissue phosphorus in 1983–83 had decreased the least of all the sites relative to the tissue phosphorus at the site in 1972. All other locations had dramatic reductions in the tissue phosphorus, indicating that the nearshore zone of these less remote sites has improved much more in a relative sense than the most remote nearshore location in Lake Ontario. The relative improvement in the nearshore

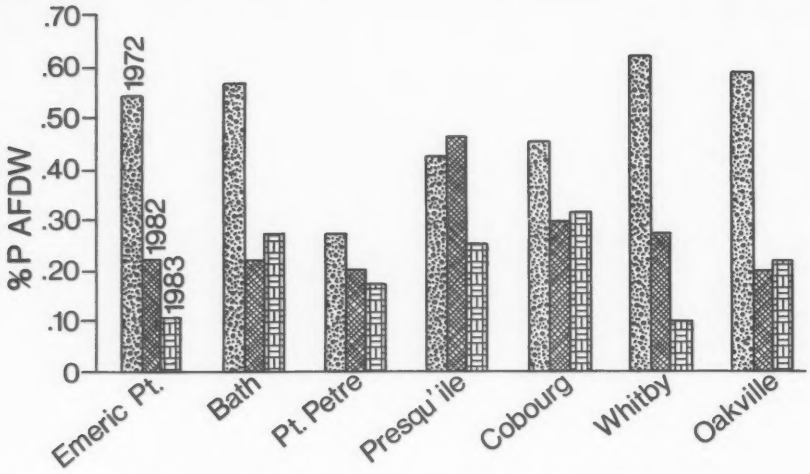

FIG. 2. *Cladophora* tissue phosphorus concentrations in 1972, 1982, and 1983.

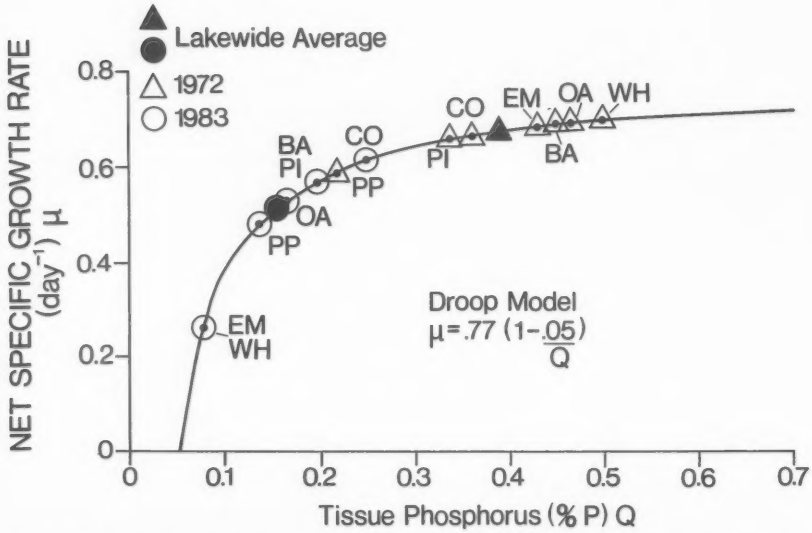

FIG. 3. Relationship between net specific growth rate (μ) and tissue phosphorus or cell quota (Q) for all stations in 1972 and 1983. Also shown are northshore averages (solid symbols).

zone of these less remote sites is to be expected because the phosphorus control programs have involved reductions of onshore loadings from the urban areas.

The relationship between net specific growth rate (μ) and tissue phosphorus (Q) (Auer and Canale 1982) takes the form $\mu = 0.77 \times (1\text{-}(0.5/Q))$ (Fig. 3). The 1972 tissue phosphorus data were situated on the plateau of the curve, indicating that phosphorus was not limiting growth of *Cladophora* in the early 1970's. The 1983 tissue phosphorus data are all located on the descending portion of the curve, indicating that phosphorus is limiting growth to a greater or lesser extent depending on the station.

Cladophora net production and tissue phosphorus were simulated for a 6-wk period using a growth model derived from Canale and Auer (1982). The model used the inputs of Secchi depth, temperature, SRP, and solar radiation which Canale and Auer found to be the significant environmental variables important for *Cladophora* growth. The tissue phosphorus predictions agreed very well with the observed tissue phosphorus. Net production for the 6 wks was averaged to give a daily average net production for each site which was then compared with the average net production at Point Petre, our most remote site (Fig. 4). A definite geographical trend is apparent for the predicted net production. Potential for growth was least at Point

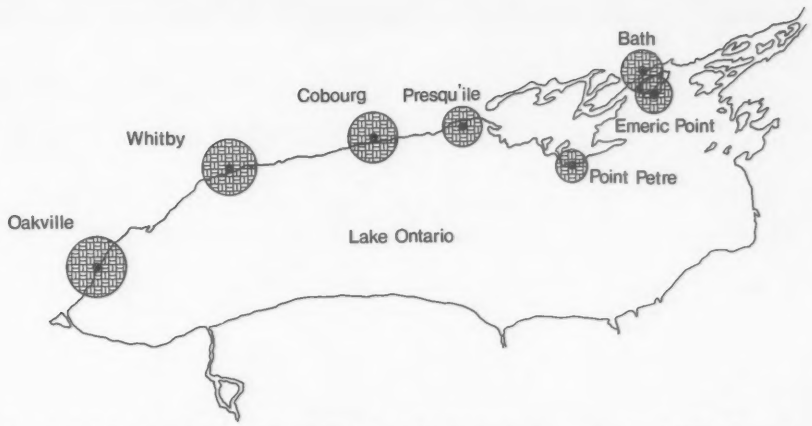

FIG. 4. Relative growth potential predicted from Secchi depth, temperature, and SRP. The circle diameter for each site is relative to the circle diameter for Point Petre.

Petre and Emeric Point and increased towards the western, more populated end of Lake Ontario. The Oakville site was predicted to have 1.7 times more growth than the Point Petre site. The trend of increased growth potential from east to west is mainly a function of SRP which increased from average values of 1.8–2.7 in the east to 5.8–7.0 μg/L in the west.

Further reductions in phosphorus loading to Lake Ontario could significantly reduce *Cladophora* populations, since the tissue phosphorus at all locations in 1982–83 was low enough to limit growth rate. Because the phosphorus reductions in the 1970's occurred at the urban centers, the affected locations improved to a greater degree than the remote locations. Even though the growth rate on an areal basis is presently limited by phosphorus, the large areas of suitable bedrock substrate in the Burlington to Toronto area may result in nuisance accumulations of *Cladophora* in the immediate vicinity depending on the frequency of storms.

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Differential Thermal and Thermogravimetric Analysis of Sediment-Forming Materials from Lake Ontario

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Differential thermal analyses (DTA) and thermogravimetric analyses (TGA) of seston, sediments, and sediment trap material from Lake Ontario were generally similar to each other but were strikingly different from those of the green alga *Chlorella pyrenoidosa*. Coinciding with the principal weight loss of carbohydrate material, the main exothermic reaction for all lake samples began at 200–250°C and peaked at 345–355°C. Trap samples varied over the season and samples from the deep traps (178 m) had exotherms which were broader with less energy content than from traps near the bottom of the metalimnion. This trend continued into the sediments. Compounds likely to be found in sediments (cellulose, chitin, and humic substances) were also analysed. The calcium carbonate endotherm which begins near 675°C distinguishes this compound from the total "ash" content. DTA and TGA can be used to detect changes in composition of lake organic matter during the sediment-forming process.

Les analyses thermiques différentielles (ATD) et thermogravimétriques (ATG) du seston, des sédiments et des matières recueillies dans le lac Ontario à l'aide de trappes à sédiments se ressemblaient généralement mais elles étaient remarquablement différentes de celles de l'algue verte, *Chlorella pyrenoidosa*. La principale réaction exothermique dans tous les échantillons lacustres a débuté à 200–250°C et a atteint un maximum à 345–355°C; cette réaction a coïncidé avec la principale perte de poids en hydrates de carbone. Les échantillons des trappes ont varié au cours de la saison; ceux recueillis dans les trappes mouillées en profondeur (178 m) ont montré des courbes exothermiques plus importantes à teneur en énergie moins élevée que les échantillons recueillis près du fond du métalimnion. Cette tendance s'est poursuivie dans les sédiments. On a aussi analysé les composés susceptibles d'être présents dans les sédiments (cellulose, chitine et substances humiques). La courbe endothermique du carbonate de calcium qui commence vers 675°C distingue ce composé du contenu total de "cendres". Les ATD et ATG peuvent être utilisées pour détecter les variations de la composition de la matière organique lacustre au cours du processus de formation des sédiments.

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Differential thermal analysis (DTA) and thermal gravimetric analysis (TGA) are techniques for studying physical and chemical changes of materials as they are heated at a specific rate in a defined atmosphere (usually air, but oxygen or nitrogen can be used). Reactions such as oxidation, pyrolysis, evaporation, or other shifts in energy state cause the temperature of the sample to differ from the inert reference material. The record of temperature differences provides the DTA profile. With TGA, the weight of the sample is recorded as the temperature is increased. Weight lost at the corresponding temperatures where endothermic and exothermic reactions occur with DTA can be used to approximate enthalpy or heat of combustion changes. TGA provides additional insights into interpretations of the commonly used "weight loss on ignition" analysis obtained by heating samples in muffle ovens. Further discussion of these techniques is provided in Smothers and Chiang (1958), Mitchell and Mackenzie (1959), Mitchell (1960), Garn (1961), Cicel (1965), Schnitzer and Hoffman (1965), Schwenker (1965), Grim (1968), Morita (1957, 1970), and Kosik et al. (1982).

No existing chemical or biological method is suitable to quantify all the organic compounds contained in the water column or the sediments. Problems with chemical techniques include poor recoveries of humic substances (Schnitzer and Khan 1972a) and the inability to distinguish bioavailable organic material. Instead of the total calories used in bioenergetic studies, thermal analysis spectra may ultimately lead to the identification of biologically useful calories.

Almendros et al. (1982) showed that the degree of transformation of the organic matter increased with depth in peat. Similarly, Balmer and Kaffehr (1980) found that the enthalpy or heat of combustion derived from concurrent DTA and TGA analysis of sewage sludge decreased and that peaks shifted towards higher temperatures during composting, aging, or stabilization over several weeks. Although commonly used by

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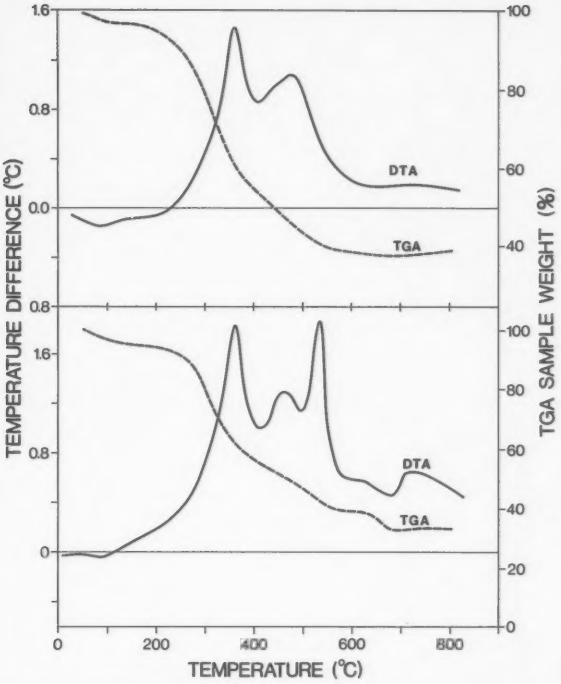

FIG. 1. DTA (Dupont 1090) and TGA (Netzsch 409) of seston samples (3.4 mg) collected on 21 June 1984 (upper panel) and 27 September 1984 (lower panel).

chemists for characterization of cellulose and other hydrocarbons, the only previous work relevant to lake ecosystems is that by Johnson (1977) who provided TGA on sediment trap samples, Buergi et al. (1981) who conducted DTA on *Pediastrum boryanum*, and Konrad et al. (1970) who investigated DTA patterns for sediments.

The following investigation was conducted to determine if thermal analysis could provide useful information to characterize biogeochemical changes as organic compounds and carbonates undergo transformations from seston to sediments.

Materials and Methods

Three differential thermal analysers were used. Most DTA experiments were conducted on a Dupont 1090 where TGA measurements were made separately on a Netsch STA 409. An older Dupont 900 also provided reliable information. Further experiments were conducted using a Netsch STA 429/409 where DTA and TGA were run simultaneously on the same sample.

Platinum thermocouples (Pt/Pt13%Rh) were used to measure the temperature of the sample and the inert reference material (calcium oxide for the Dupont 1090 and aluminum oxide for the others). Temperature calibration was made by oxidation of Sn, Ga, and Zn. Variation between replicate calibrations was less than 5°. Samples were contained in platinum crucibles.

Thermograms were obtained by heating the sample at a rate of $20°\cdot min^{-1}$ from room temperature to 900°C with an air flow of $50\,mL\cdot min^{-1}$. As pointed out by Sandermann and Augustin (1963) and Morita (1970), both the beginning of the peak and the position of the peak maximum are important. We provide the temperature of the beginning of a peak followed by the temperature of the peak maximum in parentheses.

Seston samples were obtained by continuous centrifugation (Sorval RC2B) of freshly collected Lake Ontario water from station 403 (43°35′50″ lat, 78°13′48″ long) where the maximum depth is 178 m. At this station, sediment trap material was also collected as described by Charlton (1983). Rates of sedimentation are provided in Lean et al. (1987). Sediments were sampled at a station near 403 using a Benthos gravity corer. Seston and sediment trap samples were freeze-dried but the sediment samples were air-dried. All were ground to a homogeneous particle size of less than 250 μm.

The green alga *Chlorella pyrenoidosa* was grown in 50% Bristols's medium on a 16 h day : 8 h night cycle. Other materials tested were chitin from crab shells (Sigma) and cellulose (Polysciences). Humic substances were extracted (Schnitzer and Kahn 1972b) from a mixed 1-m sediment core obtained from a midlake station.

Carbohydrate content of the sediment trap material was analyzed using the phenol – sulfuric acid method of Dubois et al. (1956).

Results and Discussion

DTA and TGA of seston collected in June and September 1984 (Fig. 1) show an initial weight loss during a small endothermic reaction to 100°C. This has been assumed to represent loss of residual moisture but can include volatilization of other materials and other reactions (Morita 1957; Schnitzer et al. 1964; Lawson and Pemberton 1965; Kodama and Schnitzer 1969; Johnson 1977). The major weight loss corresponds with the main DTA exotherm beginning near 200°C, increasing in slope by 300°C, and peaking near 360°C. The first DTA peak is followed by additional smaller peaks. Secondary exotherms begin when about 50% of the initial weight has been lost. In the September sample, the main exotherm begins at a lower temperature and the last peak is more pronounced. The residual ash weight (from TGA) was 35 and 30% for the June and September samples, respectively. If calcium carbonate were present, an endotherm at 700°C would be observed (see below). This was not found in the June sample, for the water had not warmed sufficiently, but a small endotherm exists in the September sample.

To follow the fate of organic and inorganic material as it settles from the euphotic zone, DTA and TGA were conducted (Netzsch 409) on samples collected between 8 June and 10 August 1983 from sediment traps located at 20 m (Fig. 2A) and 174 m (Fig. 2B) and from sediments (Fig. 2C and 2D). The weight loss that occurred between 200 and 700°C is similar to loss on ignition values (Table 1). The main exothermic reaction begins slightly above 100°C. This may or may not be a machine difference, as all three analyzers occasionally provided such results. The main peak is followed by secondary DTA peaks (Fig. 2B) or shoulders (Fig. 2A and 2C). The deep sediment (Fig. 2D) resulted in a broader, but shallow peak. The organic material in the 19- to 20-cm layer is about 120 ± 20 yr old (Kemp and Harper 1976) and has been shown to be decomposed to a greater extent than surficial sediments (Kemp et al. 1972).

The major endothermic peak 680–900°C corresponds to the release of CO_2 from calcium carbonate (Konrad et al. 1970; Johnson 1977). Although it began at roughly the same position, the magnitude was diminished from A though D. At 19–20 cm,

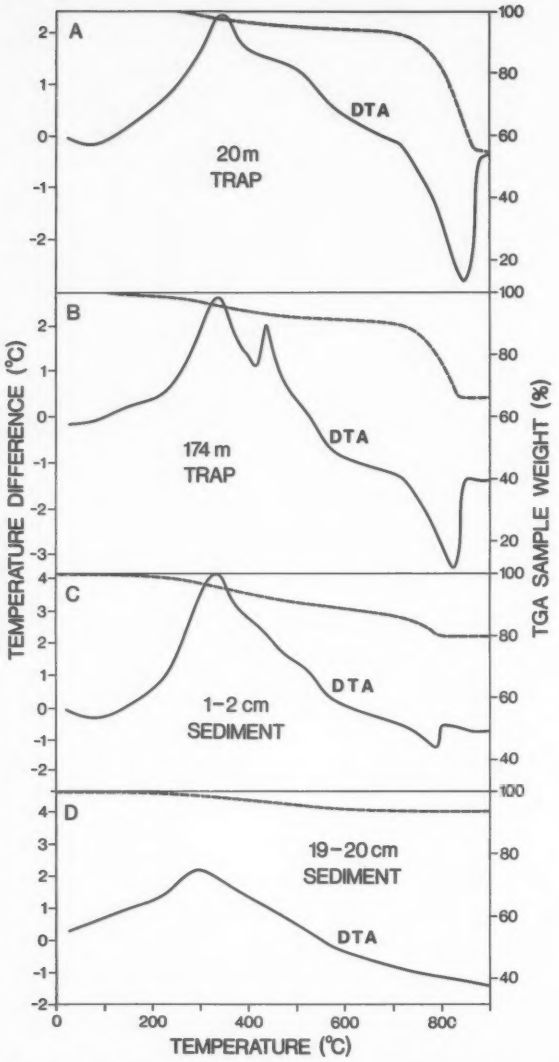

FIG. 2. DTA and TGA (Netzsch 409) for sediment trap material collected from 8 June to 10 August 1983 at a depth of (A) 20 m, (B) 174 m, (C) surficial sediment (1–2 cm), and (D) deep sediment (19–20 cm).

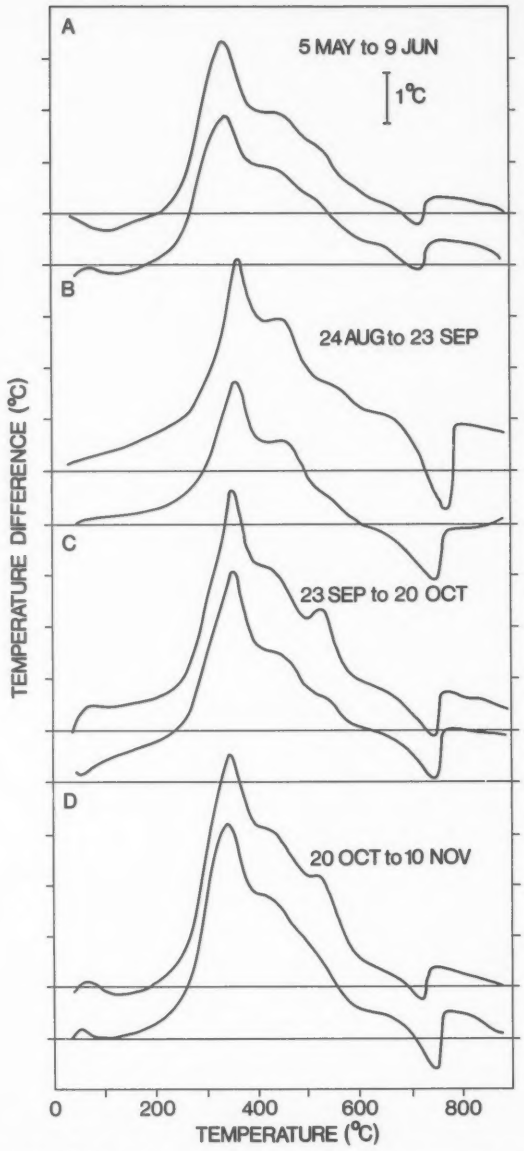

FIG. 3. DTA from 40-m (top curve of each panel) and 176-m (bottom curve of each panel) sediment traps collected from (A) 5 May to 9 June, (B) 24 August to 23 September, (C) 23 September to 20 October, and (D) 20 October to 10 November 1982. The horizontal line in Fig. 3A indicates the zero temperature difference.

no calcium carbonate endotherm was observed even though 93% of the sample remained after heating to 900°C. This observation is consistent with that of Kemp et al. (1972) who found that calcium carbonate decreased to undetectable levels at the 20-cm layer. The residual weight (Table 1) increased from seston to deep sediments but the high ash values from weight loss on ignition experiments were not due to calcium carbonate. Since no endothermic peak was observed for the seston samples (above), calcium carbonate must settle from the warmer surface waters soon after formation.

To determine if organic material changes during sedimentation, we obtained DTA curves for samples collected from the bottom of the metalimnion (40 m) and from 2 m above the sediments (176 m). Four examples are shown using the Dupont 1090 (Fig. 3) and six with the Dupont 900 instrument (Fig. 4). Background information is summarized in Table 2. These results illustrate that there were differences throughout the season but the 40- and 176-m trap material was similar at any one time. A large calcium carbonate endotherm (Fig. 4C) appears after stratification on 30 June. As above (Fig. 1), a shallow endothermal peak often began at about 60°C (Fig. 3A and 3D) but was followed by the main exothermal peak beginning at 200–250°C and reaching its maximum at about 350°C. A small

TABLE 1. Comparison of TGA analysis for seston (Fig. 1), sediment trap material collected from 8 June to 10 August 1983, and sediment 1–2 and 19–20 cm (Fig. 2). The loss on ignition (LOI) of the sample is shown along with the total weight used in the analysis. The percent weight loss during TGA is shown for the ranges of 100–700 and 700–900°C.

Material	Weight (mg)	LOI (%)	TGA weight loss (%) 100–700°C	TGA weight loss (%) 700–900°C	Residual (%)
Seston					
June	3.4	—	62.5	0	37.5
Sept.	3.4	—	67.5	0	32.5
Trap					
20 m	20.0	6.52	7.08	37.90	55.02
174 m	21.3	10.31	9.97	23.41	66.62
Sediment					
1–2 cm	20.4	13.09	13.45	5.84	80.71
19–20 cm	20.0	7.73	6.92	0	93.08

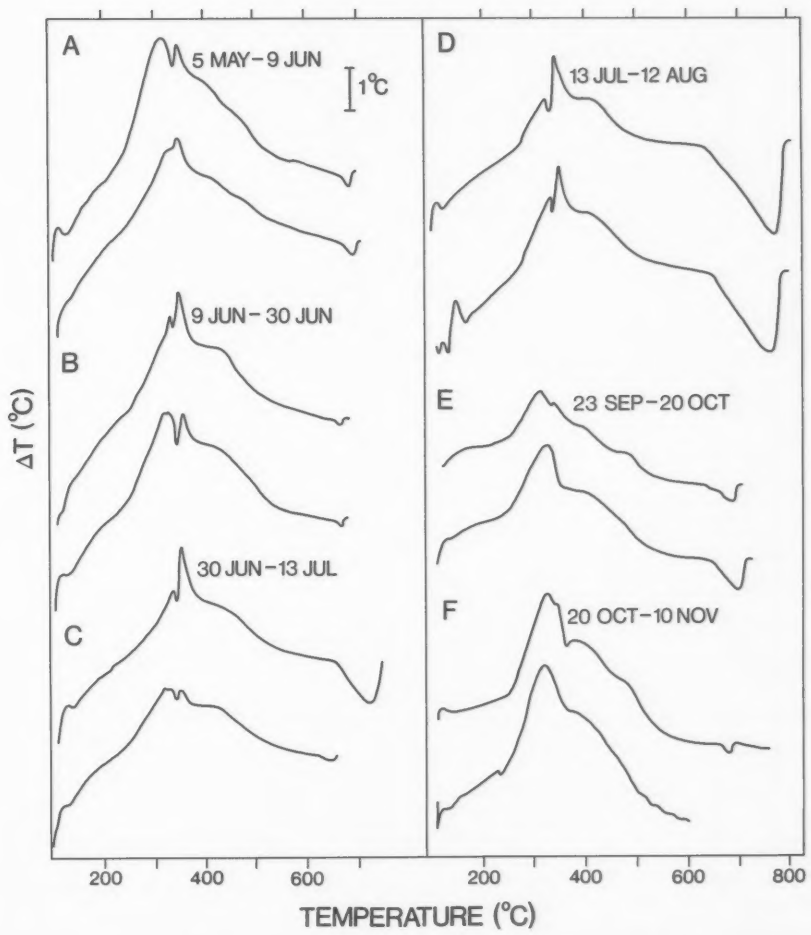

FIG. 4. DTA (Dupont 900) as in Fig. 3 for (A) 5 May to 9 June, (E) 23 September to 20 October, and (F) 20 October to 10 November, with additional data for (B) 9 June to 30 June, (C) 30 June to 13 July, and (D) 13 July to 12 August 1982. Each date includes results from 40 m (top curve of each panel) and 176 m (bottom curve of each panel).

TABLE 2. Measurements of weigth loss (LOI) of sediment trap samples. Also shown are the sample weights and the corresponding figure for DTA.

Date	Depth (m)	LOI (%)	Sample weight (mg)	Figure reference
1982				
5 May to 9 June	40	15.67	9.9,9.0	3,4
	176	14.54	8.5,9.0	3,4
9 June to 30 June	40	27.31	9.0,—	4
	176	25.57	9.0,—	4
30 June to 13 July	40	31.11	9.0	4
	176	22.04	9.0	4
13 July to 12 Aug.	40	8.47	9.0	4
	176	11.36	9.0	4
24 Aug. to 23 Sept.	40	—	—	3
	176	16.54	—	3
23 Sept. to 20 Oct.	40	31.39	—,9.0	3,4
	176	16.73	—,9.0	3,4
20 Oct. to 10 Nov.	40	31.84	—,9.0	3,4
	176	16.73	—,9.0	3,4
1983				
12 Apr. to 11 May	60	21.03	9.0	6
	100	19.88	9.0	6
	140	19.67	9.0	6
	166	19.12	9.0	6
	176	19.12	9.0	6
8 June to 10 Aug.	20	6.52	18.0	5
	60	9.63	17.1	5
	100	10.04	11.4	5
	140	10.17	11.2	5
	168	10.31	11.3	5
	176	11.37	11.4	5

shoulder exists which was more obvious with the Dupont 900 instrument (Fig. 4). Two additional exothermic peaks appeared intermittently at about 425 and 530°C. Sample weights were held constant at 9 mg (Fig. 4). Although the differences were not striking, the relative heights of the exotherms were less with 176-m material. Collecting material over 4 wk may have obscured differences; however, in view of the similarity with the seston samples which were processed immediately (Fig. 1), this is unlikely. The peak at 350°C appears to be composed of at least two separate exotherms.

DTA of trap material collected between 8 June and 10 August 1983 (Fig. 5) showed a decreasing calcium carbonate endotherm with depth and a reduction in the height of the main exotherm. The percent organic (Table 2) was lower than in the previous examples so the total weight was adjusted to keep the organic content fairly constant. DTA for the period 12 April to 11 May 1983 (Fig. 6) showed little change with depth. This is not surprising, for the water temperature was only 2–3°C and there was complete mixing of the water column.

Sediment DTA (Fig. 2) showed a lower and wider exotherm than sediment trap material. DTA on a separate core was compared with isolated humic substances (Fig. 7) as one of the more refractory organic materials expected to be found in the sediments. Like the DTA profiles from peat (Mitchell 1960; Stewart et al. 1966; Almendros et al. 1982), the DTA for humic substances isolated from lake sediments showed a two-peak system but would contribute little to the main exotherm of sediment materials. The first derivative of the DTA curve identifies points where the rate of change was most abrupt. When the same sediment samples were analyzed using the Dupont 900 (Fig. 8A and 8B), keeping the percent organic material constant (Table 2), aged material had a reduced energy content. As in Fig. 2, these results also show the reduced calcium carbonate endotherm with depth. Figures 8D and 8E provide DTA (Dupont 900) for humic substances as well as chitin (see below).

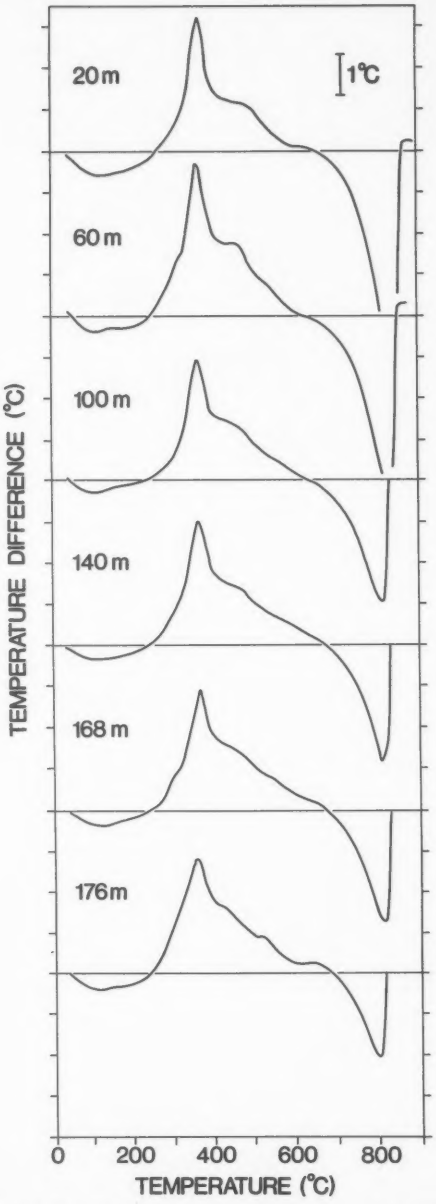

FIG. 5. DTA (Dupont 1090) of sediment trap material collected from 8 June to 10 August 1983 from depths of 20, 60, 100, 140, 168, and 176 m.

A simple relationship exists between the caloric value of the material and the peak area (e.g. Mitchell 1957). In the Lake Ontario experiments discussed above the peak area of the deep sediments was small (even though the organic content was kept

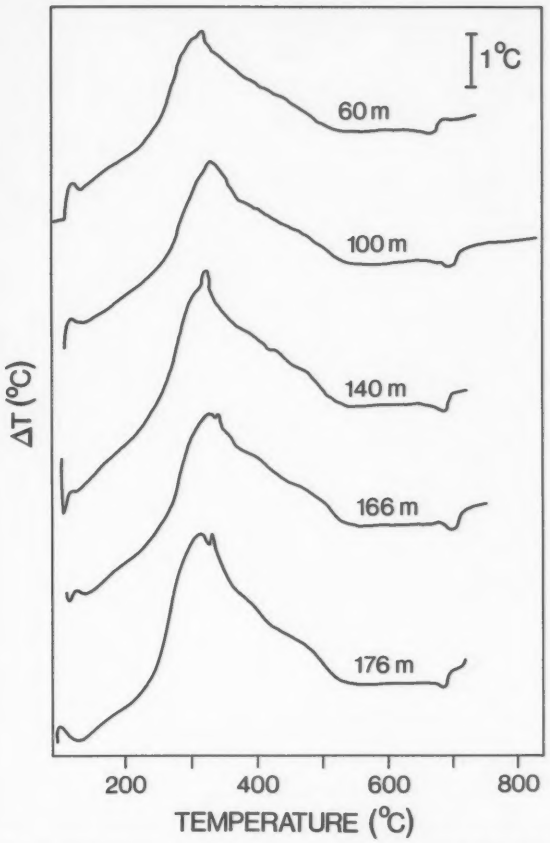

FIG. 6. DTA (Dupont 900) of sediment trap material collected from 12 April to 11 May 1983 from depths of 60, 100, 140, 168, and 176 m.

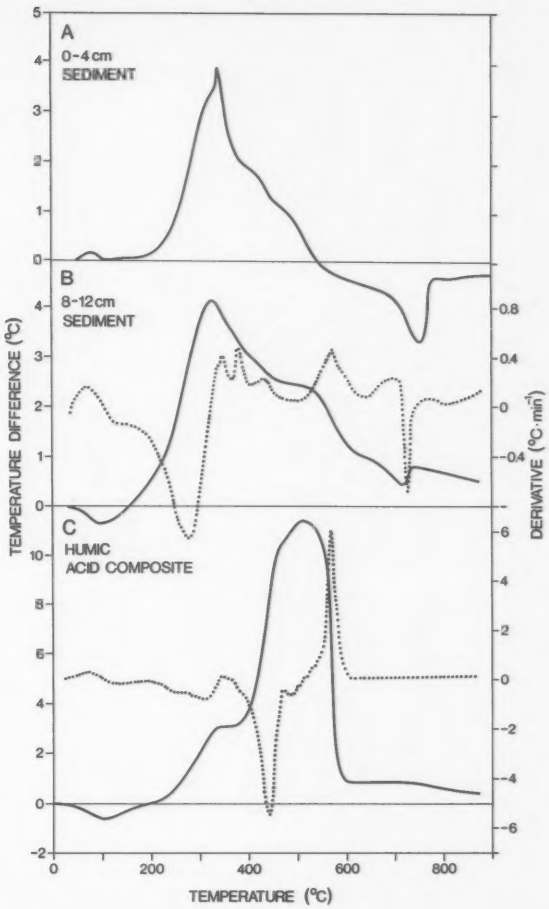

FIG. 7. DTA (Dupont 1090) for 12.2-mg sediment from (A) 0–4 cm and (B) 8–12 cm. The % LOI values were 12.83 and 9.57, respectively. Also shown is the DTA for humic substances (C).

the same). Further studies on sediments should include simultaneous TGA and DTA so that the enthalpy of the reactions can be more refined. The energy content of the organic material from sediment traps in Lake Constance did not decrease with depth but the energy content in sediments was less (Zimmermann 1983).

DTA for *C. pyrenoidosa* (Fig. 9A) was similar to that for another green algae, *P. boryanum* (Buergi et al. 1981) and to humic substances (Fig. 7) but different from DTA for seston (Fig. 1), sediment trap material, or sediments. The peak height (Fig. 9A) was a 23° temperature difference, and sample size was 28.1 mg, so the production of heat was similar to the other samples. If these observations for *C. pyrenoidosa* and *P. boryanum* prove to be typical for "healthy" algae, then the DTA for seston (Fig. 1) would suggest it contains some sediment-like material.

Cellulose, the principal cell wall component of phytoplankton, was obtained in the chemically pure form (Sigma). An exotherm (Fig. 9B) peaks at 290°C, followed by an endotherm with a minimum at 337°C and then three sharp exotherms peaking at 380, 499, and 526°C. Mixed with trap material, the cellulose contributed to the high initial exotherm (Fig. 9C) but the other peaks were less obvious. When a pure compound has been mixed with other materials, peak shifts have been observed (Smothers and Chiang 1958). Sandermann and Augustin (1963) also found that the endothermal peak of pure cellulose was obscured in a mixture of cellulose and lignin or hemicellulose due to overlapping of endothermal and exothermal peaks. Some compounds may act as catalysts accelerating the reaction and lowering the temperature where decomposition occurs. Sandermann and Augustin (1963), as well as Kosik et al. (1982), found that the DTA curve of pure cellulose in air contained an exothermal peak at 340°C. Mitchell (1960) found a DTA curve for cellulose with two peaks at 320 and 460°C and he considered that a temperature difference of about 100° may be due to differences in particle size and crystallinity.

Discarded exoskeletons have been observed in trap material and lake sediments, so chitin, a substance in the zooplankton carapace, was analyzed. The first exotherm (Fig. 9E) peaked at 365°C, had a shoulder at 460°C, and a second exotherm at 566°C (see also Fig. 8E). The DTA for a relatively pure substance gives sharp peaks. Mixed with trap material (Fig. 9F), the exotherms were less distinct but caused the mixture to be different from that for trap material alone (Fig. 9D).

Carbohydrate content was measured during DTA and TGA. Samples were heated to specific temperatures, removed, cooled

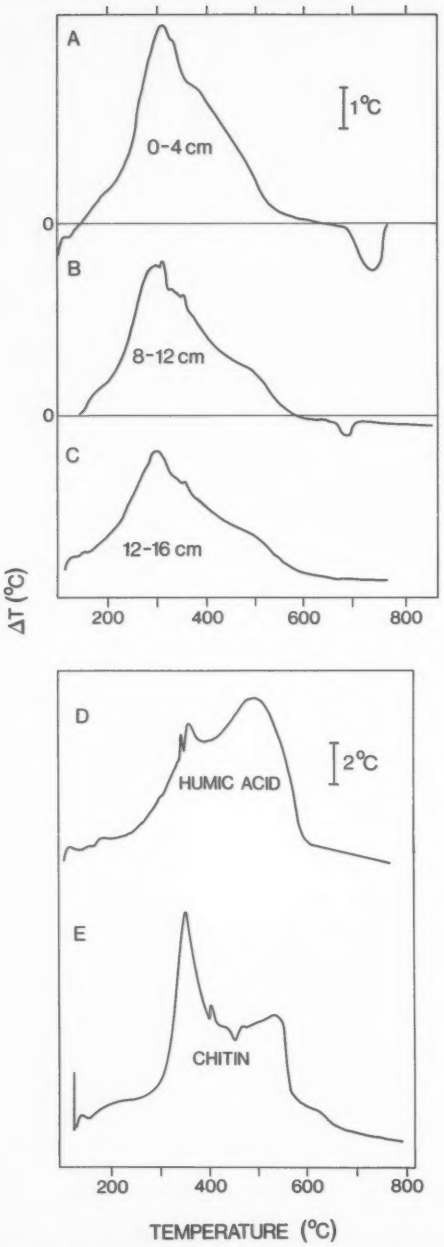

FIG. 8. DTA (Dupont 900) for (A) 16-mg sediment from 0–4 cm, (B) 13 mg at 8–12 cm, (C) 12.5 mg at 12–16 cm, (D) humic substances, and (E) chitin.

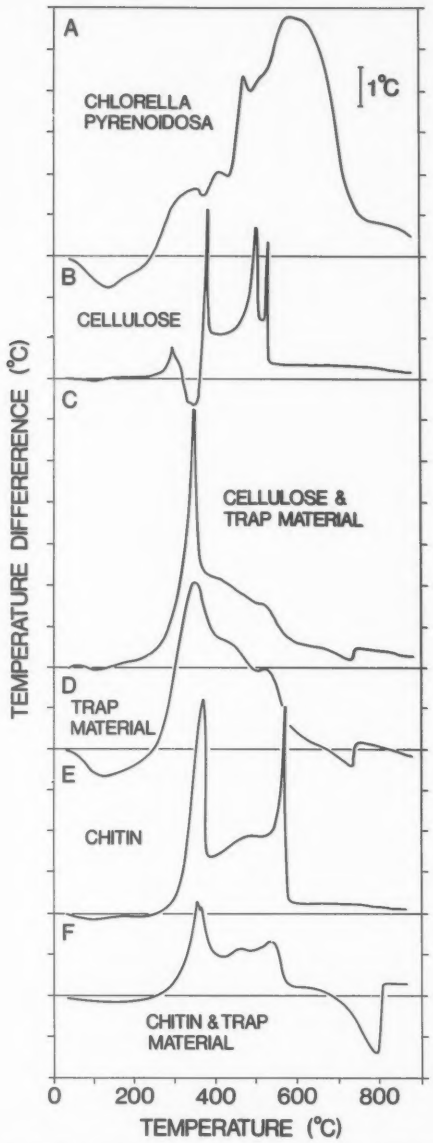

FIG. 9. DTA of (A) *Chlorella pyrenoidosa* (28.1 mg), scale ×4 = °C, (B) cellulose (8.8 mg), scale ×4, (C) a mixture of cellulose (18.4%) with sediment trap material (6.2 mg total weight), (D) the sediment trap material alone (9.0 mg), scale ×1 (sample collected between 20 October and 10 November, (E) chitlin (10.5 mg), scale ×2, and (F) a mixture of chitin (19.3%) and sediment trap material (9.3 mg total weight).

rapidly, and analyzed in duplicate (Fig. 10). By the end of the experiment the weight loss was approaching that measured in a muffle oven (loss on ignition). Carbohydrate was lost during the principal exotherm of trap material. Nevertheless, most of the other organic materials were also lost at this time. Almendros et al. (1982) concluded that the first peak at about 350°C in their DTA of peat was correlated with the carbohydrate content, but in future experiments, analysis of protein and lipids should also be made.

Each organic or inorganic compound influences the thermal characteristics of a mixture of compounds. Only the integrated result is observed, so it is impossible to isolate the specific effect of any one compound in the mixture. Nevertheless, the overall fingerprint can be useful in the characterization of the material and suggests directions for more specific chemical

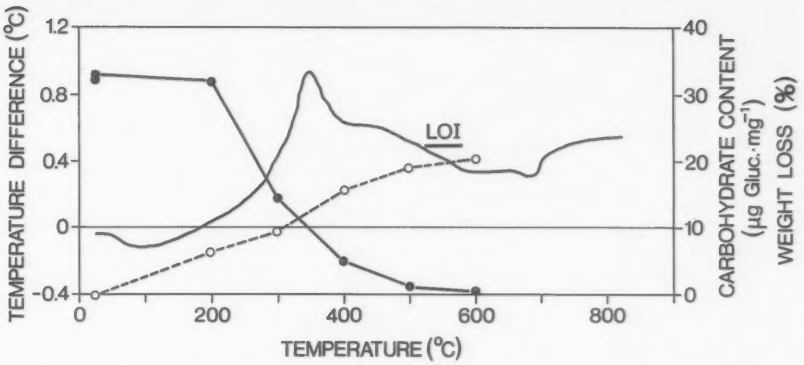

FIG. 10. DTA (Dupont 1090) and corresponding TGA (Netzsch 409) at specific temperatures for a 60-m sediment trap sample obtained in June 1983. Also shown is the day weight carbohydrate content and corresponding loss on ignition (LOI) value.

analysis. If the differences between algae and seston prove to be consistent, then seston contains a high detrital component. Furthermore, because DTA and TGA can be measured simultaneously, the enthalpy of specific peaks can be calculated. Combined with gas chromatography and mass spectrometry, it may yet be possible to distinguish biologically available calories and identify the transformations of organic materials which occur in lake ecosystems. Certainly, the information obtained from DTA and TGA is more informative than total calories from bomb calorimetry.

In summary, exothermic reactions characteristic of the oxidation of organic substances were complete at 600°C. The weight loss up to that point, measured by TGA, is similar to the amount of organic material measured using a muffle furnace for 2 h at 550°C (Tables 1 and 2). This provides some confidence in using 550°C for particulate organic carbon analysis except for samples containing magnesium carbonate. This compound decomposes at only 350°C liberating carbon dioxide (Konrad et al. 1970). No release of carbon dioxide from calcium carbonate occurs until higher temperatures are reached. This shows that for samples without magnesium carbonate, acid washing of filters for particulate organic carbon analysis is unnecessary (and may even cause artifacts due to cell damage). Almost all the organic carbon is burned before 550°C.

Konrad et al. (1970) found thermograms for lake sediments similar to ours. Almendros et al. (1982) observed that peat from different locations and depths had a common exotherm at 350°C but their second or third exothermal peaks were at different temperatures. Both are similar to the thermal analysis profiles for sewage sludge (Balmer and Kaffehr 1980). In other words, the products which sediment from Lake Ontario matter have features similar to sewage sludge and peat.

Acknowledgments

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Time of Onset of Full Thermal Stratification in Lake Ontario in Relation to Lake Temperatures in Winter

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Rodgers, G. K. 1987. Time of onset of full thermal stratification in Lake Ontario in relation to lake temperatures in winter. Can. J. Fish. Aquat. Sci. 44: 2225–2229.

Using records from 1965 to 1985 including temperature data from vessel surveys and remote sensing by aircraft and satellite, relationships are explored amongst winter severity, early spring water temperature, and the date on which thermal stratification is established throughout the lake. One extreme event stands out in 1983, in association with the anomolous extent of the El Niño current in the Pacific Ocean. Winter conditions in 1983 in Lake Ontario appear to be within the warmest 5% of winters on record: this is reflected in air and water temperatures and in the very early onset of full thermal stratification of Lake Ontario. The data provide a means of assessing the spring conditions of any particular year and also provide some predictive capability should one wish to schedule experiments to take advantage of particular thermal structures in spring or early summer.

A l'aide de données recueillies de 1965 à 1985 (y compris la température relevés de navire et par télédétection à partir d'aéronefs et de satellites), on a étudié les rapports entre la rigueur de l'hiver, la température de l'eau au début du printemps et la date d'établissement de la stratification thermique dans le lac Ontario. Un événement particulier, lié aux anomalies du courant El Niño dans l'océan Pacifique, marque l'année 1983. Cette année-là, les conditions hivernales dans le lac Ontario se situaient parmi les plus chaudes enregistrées au cours de 5 % des hivers pour lesquels on dispose de données : ces conditions ont été exprimées dans les tampératures de l'air et de l'eau et le début très précoce de la stratification thermique complète du lac Ontario. Les données fournissent un moyen d'évaluer les conditions printanières présentes au cours d'une année donnée et une capacité de prédiction si l'on veut planifier des expériences pour tirer parti de conditions thermiques particulières au printemps ou au début de l'été.

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Now that a good length of record for physical, biological, and chemical data is available from Lake Ontario, efforts have been intensified to refine the interpretation of trend data in relation to the phosphorus control program. That interpretation may depend on the varying thermal characteristics of the lake.

The relationships among water temperature, biomass, and primary production have been presented (Stadelmann et al. 1974) for an inshore and an offshore station in Lake Ontario. They have illustrated the major influence of deep circulation associated with the "turnover" of late winter and early spring. This deep vertical circulation persists in the central deeper part of Lake Ontario long after the inshore waters have warmed and stratified, sometimes well into early summer. The zone of 4–6°C surface water, the "thermal bar" (Rodgers 1965), separates the stratified and deeply circulating portions of the lake.

The date when stratification of Lake Ontario is complete ranges from mid-May to early July. Consequently, estimates of total biomass or interpretations of time series records at any location in the lake must take these climatic variations into account.

This report describes the year-to-year differences in late winter and spring water temperatures for Lake Ontario from 1965 to 1985. The relationship between these two thermal regimes and the conditions that generate them are examined.

Data Sets

Temperatures in the Deep Part of the Lake

Data have been assembled from the records of vessel surveys on file with National Water Research Institute at the Canada Centre for Inland Waters in Burlington. Vessel surveys provided complete temperature profiles from which were extracted the temperatures in the top 100 m of the lake in the deepest portion of the lake for dates around April 1 of each year (Table 1). Most surveys were carried out during the first week in April, but interpolation between mid-March and mid-April surveys was necessary in some cases. In this analysis, the type of information generated in an earlier report (Rodgers and Sato 1970) is reproduced to extend the record back to 1965.

The temperature of the top 100 m is an indication of the heat content of the lake in early April. Often the same temperature prevailed to 120 or even 160 m. But in all years, there was a slight inverse stratification. Bottom temperatures (degrees Celsius) (nearly 200 m of depth) were as much as 2° higher than surface temperatures about 15% of the time and less than 1° higher than upper layer temperatures 50% of the time.

TABLE 1. Winter/spring Lake Ontario water temperatures east of 77°45′W for total c

Survey dates	Number of survey sites providing temperature profiles	Range of temperatures in top 100 m	Average (°C)	A t (f h
1965 April 6	(for 1965–69, see	1.7–2.2	1.9	
1966 March 30	paper by Rodgers and	2.0–2.7	2.3	
1967 March 28	Sato 1970)	1.9–2.6	2.3	
1968 April 2		1.3–1.7	1.5	
1969 April 2		1.4–1.9	1.6	
1970 April 3–5	6	1.1–1.9	1.2	
1971 April 1–2	4	0.9–1.3	1.1	
1972 April 5–7	12	1.1–2.0	1.6	
1973 April 4–5	14	2.3–2.8	2.5	
1974 April 3–4	4	2.2–2.7	2.4	
1975 April 11–12	7	2.3–2.6	2.5	
1976 April 8	9	2.0–2.2	2.1	
1977 (1) March 17–18	9	0.1–0.6	0.3	
(2) April 13–14	8	0.6–1.1	0.8	
1978 (1) March 21–22	9	0.2–2.0	0.5	
(2) April 12–13	9	0.7–1.5	1.1	
1979 (1) March 22–23	9	1.1–1.7	1.3	
(2) April 11–12	9	1.4–1.9	1.6	
1980 March 26–27	9	1.3–2.2	1.8	
1981 (1) March 20	9	1.2–1.9	1.4	
(2) April 8–9	9	1.8–2.2	2.0	
1982 March 30–31	5	1.0–1.4	1.1	
1983 April 6–7	9	3.1–3.8	3.4	
1984 April 4–5	9	1.7–2.1	1.9	
1985 April 3–4	8	1.4–1.9	1.7	

or total depths >140 m.

(°C)	April 1 temperature (average adjusted for normal heating rate) (0°C)	Date of disappearance of thermal bar (estimated as text describes)	Mean air temperature December to March preceding April 1 of each year (Pearson International Airport, Toronto) (°C)
	1.7	June 21	−4.8
	2.3	June 8	−3.3
	2.4	June 14	−4.4
	1.5	June 22	−4.5
	1.6	June 21	−4.6
	1.1	June 17–18	−6.4
	1.1	June 25–30	−5.7
	1.4	June 28–30	−4.8
	2.4	May 26 – June 2	−2.9
	2.3	June 14–17	−4.8
	2.1	May 31 – June 3	−2.8
	1.9	June 11–16	−4.4
	0.5	June 25–30	−5.8
	0.7	June 21–25	−6.7
	1.4	June 20–25	−4.9
	1.9	Before June 15	−4.0
	1.8	June 5–10	−4.7
	1.1	July 2–5	−5.7
	3.2	May 10–11, May 18–20	−1.5
	1.8	June 3–7	−5.6
	1.6	June 13–18	−3.5

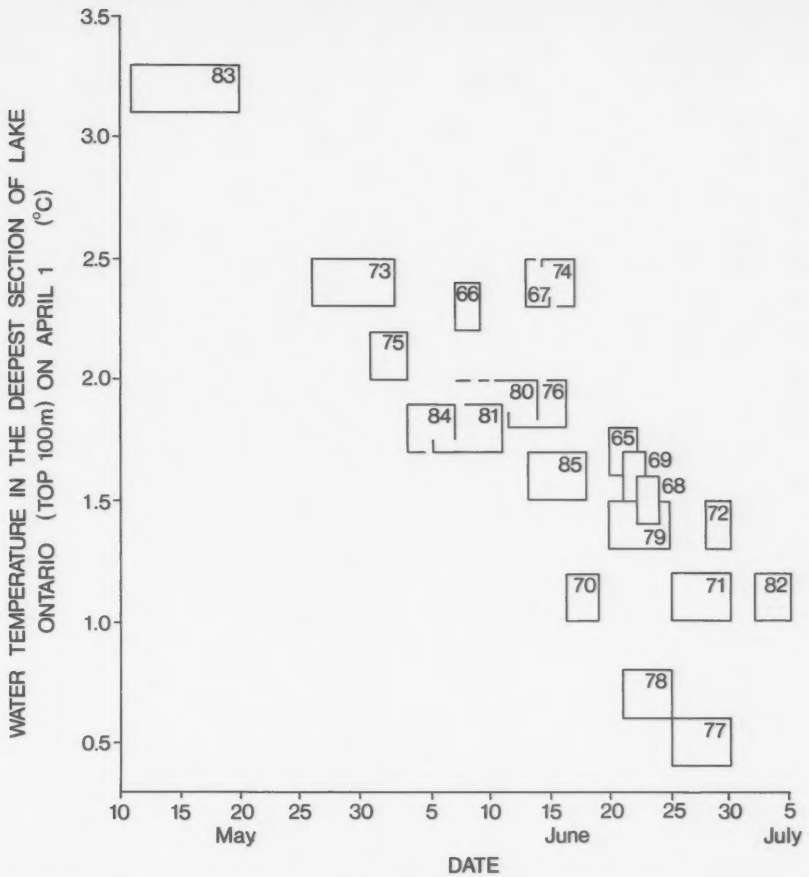

FIG. 1. Date of full stratification or disappearance of the surface 4°C isotherm as a function of the April 1 water temperature in the deepest basin of Lake Ontario just east of 77°45'W.

Adjustment for time trends in temperature is required where there is not a survey close to April 1 and surveys do not bracket that date. On the average, surface temperatures in Lake Ontario rlse 1° between mid-March and Mid-April. Therefore, changes of 0.2° per week are typical of this period. An adjusted mean upper layer temperature for April 1 of each year is tabulated using the median temperature observed and an adjustment of 0.2° per week where it was necessary (Table 1, column 5). The height of the "box" used to represent each data point in Fig. 1 reflects the uncertainty in this estimate.

Date of Full Stratification (or of Disappearance of the Thermal Bar)

The date at which the lake becomes fully stratified was estimated (Table 1, column 6). Data from ship surveys were used in conjunction with airborne and satellite radiation thermometry data as analyzed and reported by the Hydrometeorology Division of the Canadian Climate Centre (e.g. Irbe and Saulesleja 1982). Generally there are many more satellite data charts than ship surveys.

To be precise about the date of full stratification is difficult. Measuring surface and near-surface temperatures daily over all the lake from mid-May to early July is impractical. Ship surveys take several days to complete. Satellite data are widely spaced in time and are often interrupted by cloud or fog. Hence, the data generally only allow bracketing of a 4- to 7-d period during which the stratification became complete. This uncertainty is reflected in the width of the "box" used to represent each data point in Fig. 1.

Mean Air Temperatures

Mean air temperatures for the 4 mo preceding April 1 of each year were extracted from of the Atmospheric Environment Service of Environment Canada (1965–85) for Pearson International Airport (Toronto) and entered in column 7 of Table 1.

Discussion

Winter Temperatures

The heat content of Lake Ontario at the beginning of April has a major influence on the progress of thermal stratification. The heat content is, of course, the integral of several energy exchange processes over all prior time (Rodgers and Anderson

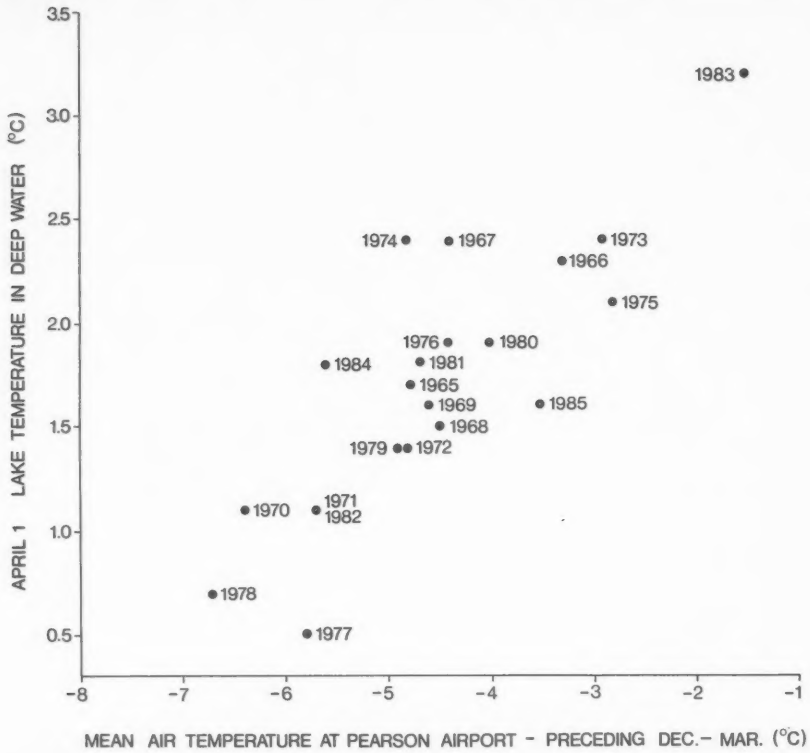

FIG. 2. Relationship between the mean temperature in the deep waters of Lake Ontario on April 1 and the mean air temperature at Pearson International Airport in the preceding winter months of December–March.

1961). There is feedback from the lake in response to strong heating or cooling rates. And there is a response time of the lake in reaching an equilibrium with atmospheric conditions. That response time depends on the effective depth of the lake. That is, the response time can depend on the depth to the bottom of the lake when the lake is vertically mixed to a thermocline or chemocline when there is density stratification.

The response time also depends on changes due to ice cover that insulate the lake from mixing and heating or cooling. It is not immediately obvious what the net impact on heat content might be with ice cover because several ice types are formed, and ice is frequently moved, broken, and rafted by the wind.

Nonetheless, air temperature correlates with some of the extreme events that establish the nature of thermal stratification or the extent of ice formation. This suggests that a simple air temperature index is a useful first step. One notes the success reported by Richards (1963) and by Assel et al. (1985) in using accumulated degree-days of freezing or a mean air temperature, respectively, to estimate the amount of ice cover in the Great Lakes. Assel et al. (1985) used the longer-term records of air temperature at land stations to supplement a very short record of ice cover observations to estimate the frequency of occurrence of various percentages of ice cover.

Hence, to assess winter severity for Lake Ontario, a mean air temperature was calculated for the 4 mo prior to April 1 of each year (Fig. 2). This 4-mo period encompasses the 3 mo when mean temperatures are almost always below freezing and the month prior to April 1 when, on the average, warming starts and ice breakup is well advanced.

The data in Fig. 2, through least squares analysis, can be represented by the equation

$$Tw = 3.62 + 0.42Ta$$

where Tw is the temperature of the top 100 m of the water column on April 1 in the deepest east-central basin of Lake Ontario and Ta is the mean air temperature as defined above. The correlation coefficient is 0.84.

Spring Water Temperatures

Generally, full stratification arrived earlier when April 1 water column temperatures were higher (Fig. 1). A least squares analysis of data yields the following equation:

$$\text{Date} = 102 - 15.3Tw$$

where "Date" refers to the day in which full stratification takes place (measured from April 1 inclusive) and Tw is defined as above. The correlation coefficient is -0.83.

However, prediction of the date of disappearance of the thermal bar is less precise than an earlier report suggested (Rodgers and Sato 1970). In the 21-yr record, it appears that the average date on which full stratification takes place is June 15. The two extremes are the first week in July (1982) and mid-May (1983).

The 1983 conditions warrant an extra word. During this period the air temperatures in the Great Lakes basin were unusually elevated, ice cover was the least on record, and the thermal bar disappeared very early. The date of stratification was also quite indistinct. It appeared from satellite records that the 4°C isotherm disappeared, reappeared, and then disappeared a second time. In addition, horizontal surface temperature gradients associated with the 4–6°C isotherms were particularly weak in 1983.

The unusual ice conditions in the preceding winter prompted Assel et al. (1985) to assess how this winter compared with others. They analysed 200 yr of air temperature records to calculate a winter severity index and concluded that the winter of 1982–83 ranked 10th warmest in the 200-yr record. This suggests that the 1965–85 record (Fig. 1 and 2) may not be atypical, but that 1983 was a rather singular year in this 21-yr data set.

However, before straining the analysis too far, it should be noted that there are data points that suggest the need for a more detailed analysis of the heat energy exchange, runoff characteristics, major wind events, and antecedent heating factors. There is some indication, for example, that the springs in 1970, 1975, and in 1977 each had somewhat higher heating rates, while the springs of 1982 and 1972 experienced lower heating rates (W. Schertzer, Canada Centre for Inland Waters, and A. Sawchuk, University of Toronto at Scarborough, pers. comm.). If the heating were closer to the average in these 5 years, the data points in Fig. 1 for these years would shift so as to be more in line with the other data, thus reducing the scatter. Should more detailed analyses be required, such factors would have to be taken into account.

The impact of major wind events on thermal stratification has been detailed for 1972 in the IFYGL studies (Aubert and Richards 1981). Interestingly, however, the impact of hurricane Agnes, a 200-yr storm event, is not evident in the data for Fig. 2, although it altered the horizontal temperature patterns remarkably.

Conclusions

The dates on which thermal stratification is complete in Lake Ontario differ from year to year by as much as 50 d. A major factor determining this date is the heat content of the lake in late winter, expressed here as the average temperature of the top 100 m of the lake over the deepest part of the east-central basin of the lake.

Biological and chemical processes dependent on the degree of vertical mixing in the lake will be dependent on the progress of stratification, and hence, comparison of different years in any trend analysis will require attention to this factor.

Acknowledgements

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The Lake Ontario Life Support System

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Primary productivity provides most of the energy to support aquatic food chains. The rate is not only influenced by available solar radiation but also by temperature, availability of phosphorus, and the influence of physical mixing processes. The special features of Lake Ontario such as changes in phosphorus concentration, calcium carbonate precipitation, and silica deficiency on primary productivity, concentration of particulate carbon, and chlorophyll are discussed. Our lack of understanding of food chain and nutrient regeneration processes is illustrated through our failure to balance carbon production with losses through zooplankton grazing and sedimentation. It was demonstrated, however, that bacteria are not responsible for nutrient regeneration through "mineralization" but nutrients are effectively recycled in the water column at the second and third trophic levels.

La productivité primaire fournit la plus grande partie de l'énergie nécessaire aux réseaux alimentaires aquatiques. En plus d'être influencé par l'énergie solaire disponible, le taux est soumis à l'influence de la température, du phosphore disponible et des processus de mélanges physiques. Les auteurs examinent les caractéristiques du lac Ontario dont les variations de la concentration de phosphore, le dépôt de carbonate de calcium et la carence en silice sur la productivité primaire, la concentration de carbone particulaire et de chlorophylle. Les auteurs n'ont pu établir un équilibre entre la production de carbone et sa perte par broutage du zooplancton et sédimentation; ceci illustre le manque de compréhension des processus liés au réseau alimentaire et au renouvellement des bioéléments. Les auteurs ont toutefois démontré que les bactéries ne sont pas responsables du renouvellement des bioéléments par "minéralisation" mais que les bioéléments sont recyclés dans la colonne d'eau aux deuxième et troisième niveaux trophiques.

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A lake ecosystem is maintained by the input of solar energy which, through the process of photosynthesis, is converted to organic carbon. Nevertheless, the fate of the carbon, both particulate and dissolved, is poorly understood (Tilzer 1984; Smith et al. 1984; Forsberg 1985). Furthermore, while literature on quantitative relationships between light intensity and total primary production is copious (see reviews by Harris 1978, 1984; Talling 1984), only recently has attention been focused on specific end products of photosynthetic carbon fixation (Morris and Skea 1978; Konopka and Schnur 1981; Cuhel et al. 1984; Jensen 1985; Lancelot and Mathot 1985; Cuhel and Lean 1987). Investigations of the flow of fixed carbon into specific biopolymers of carbohydrate, lipid, and protein may serve as a means of assessing the nutritional *status* of the phytoplankton and their nutritional *value* as food for herbivores (Cuhel and Lean 1987).

Usually less than 2% of the incoming solar energy is used in photosynthesis. The remainder affects water temperature and, together with wind stress, determines the mixing depth and current velocities (Simons and Schertzer 1987). These variables affect both the quantity and species composition of the phytoplankton. The sequence of populations is basically controlled by the physical environment, by mean flow (advection) and turbulence (mixing) (Margalef 1978). Any appearance of succession would be the result of an orderly shift in the way environmental control is exercised. Turbulence caused by wind and waves at the surface propagates toward deeper layers but is restricted by thermal stratification. When the mixing depth

exceeds the depth of the euphotic zone, the biomass is controlled by physical rather than chemical (nutrients) factors (see Harris 1986 for review).

Phytoplankton biomass exists as the net result between rates of production and consumption. Too often, nutrient control (bottom up) has been used as the sole explanation for changes in biomass. As a result of the increased fish biomass in Lake Ontario, zooplankton grazing may have increased and altered the plankton size distribution and sedimentation rates. These "top down" effects (Carpenter et al. 1985; McQueen et al. 1986) can alter the carbon flow through the ecosystem. Furthermore, since the energy flux varies hourly, diurnally, and seasonally with a lag between energy input and biological response, population oscillations are to be expected.

An additional, but often overlooked, source of energy is the input of particulate and dissolved organic carbon from the air and the drainage basin. While sewage treatment plants and industries have made attempts to reduce their organic loadings, other inputs still occur but are poorly quantified. The relative importance of excreted labile organic carbon by the autotrophic community (Williams 1981; Azam et al. 1983) and by zooplankton (Olsen et al. 1986b) has yet to be established. In Lake Ontario, little is known about the heterotrophic microflagellates and the bacteria on which they feed in Lake Ontario (Pick and Caron 1987). In marine ecosystems, the contribution of bacterial production is unresolved. It may be either insignificant (Ducklow et al. 1986) or vitally important (Fuhrman and McManus 1984). Furthermore, ammonium excreted by animals may also provide energy to support part of the heterotrophic community (Lean and Knowles 1987).

The aim of this paper is to examine the combined effect of physical processes and nutrient availability on rates of carbon production compared with carbon losses through zooplankton grazing and sedimentation. These observations are not specific to Lake Ontario but can be applied to other lakes and oceans. The results do not represent the final chapter on ecosystem processes but rather focus attention on areas where our understanding is incomplete.

Materials and Methods

Samples were collected at northshore station 401 where the water was 38 m deep, at midlake station 403 (178 m), and less frequently at the southshore station 405 (38 m). Niskin bottles (6 L) were used on a Rosette sampler equipped with an electronic bathothermograph. The depths sampled were of 1, 5, 10, 15, and 25 m as well as at each 25-m interval thereafter including bottom minus 10 m and bottom minus 2 m. The water was transferred to 10-L polyethylene bottles which were subsampled for the various LONAS analyses within 15 min of collection (Lean 1987).

Analyses of soluble reactive phosphate (SRP), nitrite, nitrate, and ammonium were performed usually within 2 h using a Technicon II analyser, but total filtered Kjeldahl nitrogen (TKN), dissolved inorganic carbon (DIC), and dissolved organic carbon (DOC) were conducted on samples stored in acid-washed glass bottles that had been thoroughly rinsed with distilled water. Samples stored in polyethylene bottles were analysed for soluble reactive silicate (SRS), calcium, sulfate, and other major ions. For phosphorus analyses, filtered (Sartorius 11103) and unfiltered samples were stored in glass bottles, preserved using 1 mL of 30% sulfuric acid and later digested using the persulfate method (Environment Canada methods manual). As in the IFYGL studies (Stadelmann and Fraser 1974), chlorophyll *a* was measured by filtering the plankton on GF/C filters and extracting with 90% acetone. Chlorophyll concentrations, not corrected for phaeopigments, represent averages over at least three sampling periods during a 2-d period. Occasionally, all data collected over several days are shown to illustrate short-term changes. After filtering samples through precombusted (500°C) Whatman GF/C filters, particulate organic carbon (POC) and nitrogen were analysed using a Hewlett-Packard CHN analyser.

The numerical model of Fee (1984) was used to estimate integral primary production. Semimonthly photosynthetic rates were determined on 5-m water by incubating samples with ^{14}C-labeled bicarbonate in 250-mL polycarbonate bottles at five light levels and in the dark. A fluorescent street lamp was used as the light source with attenuation by fiberglass screens. After 2–3 h, samples were collected on 0.45-μm Sarorius 11306 cellulose nitrate membrane filters. Primary production estimates were calculated as described by Lean and Burnison (1979). Results were in agreement with data obtained independently by Cuhel and Lean (1987) using Whatman GF/F filters for subcellular fractionation. When combined with transparency and solar irradiance data, an estimate for areal production was obtained (Fee 1973). A LiCor quantum sensor was used to measure light intensity.

Sediment traps consisting of five core tubes (7 cm in diameter × 106 cm long) were suspended on an aluminum frame attached to a cable held taut between an anchor and a subsurface float (Charlton 1983). Samples, usually collected every 2–3 wk from station 403, were freeze-dried for analysis of POC, weight loss on ignition, calcium, nitrogen, and phosphorus (Environment Canada methods manual).

Zooplankton filtering rates were measured (Haney 1971) by lowering a 10-L grazing chamber to depths throughout the water column and releasing ^{32}P-labeled *Chlorella pyrenoidosa* for periods of up to 10 min. Zooplankton were collected on 64-μm Nitex screens. Zero time controls were subtracted for each depth. Rates were averaged from measurements taken at several times throughout the day.

Results and Discussion

Temperature

Water temperature controls the upper limit for algal productivity in many aquatic systems (Eppley 1972) including Lake Ontario (Stadelmann et al. 1974). Not only is the total productivity less when the water is cold, but protein synthesis is reduced from 20% of total production in summer to less than 5% when the water is cold (Cuhel and Lean 1987). Even the number of heterotrophic bacteria and autotrophic picocyanobacteria correlates with temperature (Caron et al. 1985b; Pick and Caron 1987). Furthermore, when the mixing depth exceeds the depth of the euphotic zone, the plankton are in the dark much of the time and their growth may be light limited (see Margalef 1978; Harris 1986 for review). Under such conditions, changes in nutrient loading would have little effect.

Temperatures recorded during collection of water samples were related to changes in the concentration of calcium, phosphorus, SRS, chlorophyll, and POC (Fig. 1–4). Inside the thermal bar, temperatures at the northshore and southshore stations increased rapidly from less than 2°C in April to 13°C before the end of June, while offshore temperatures remained

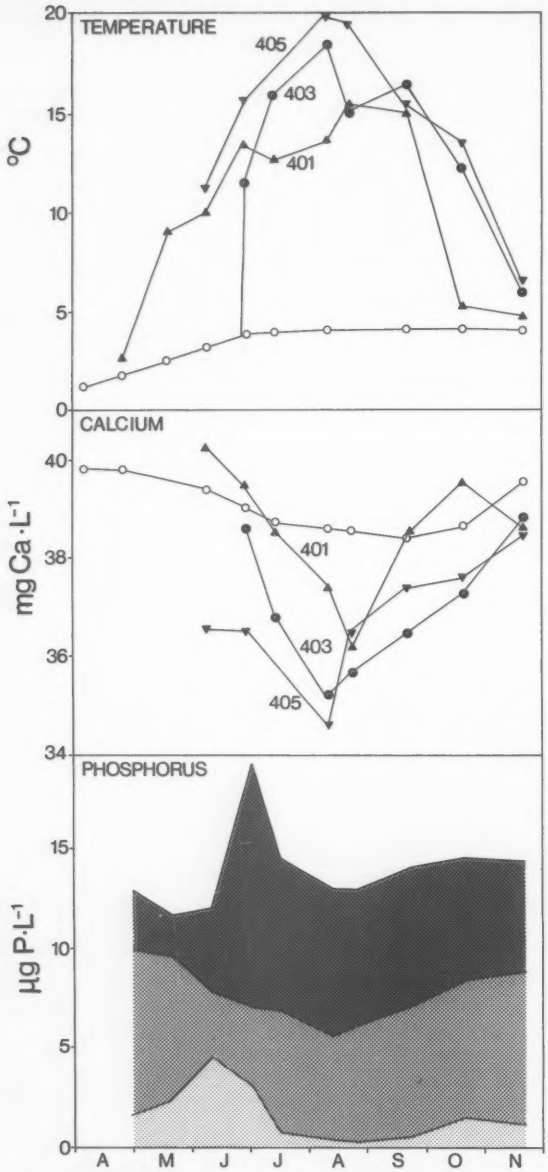

FIG. 1. Seasonal changes in epilimnetic temperatures (top) and calcium concentration (middle) at stations 401, 403, and 405 along with mean hypolimnetic temperatures and calcium concentration (open symbols) at 403. Given on the bottom panel are concentrations of SRP (light), SUP (darker), and particulate P (darkest). Water samples were collected from 5 m. Data are from LONAS cruises in 1982.

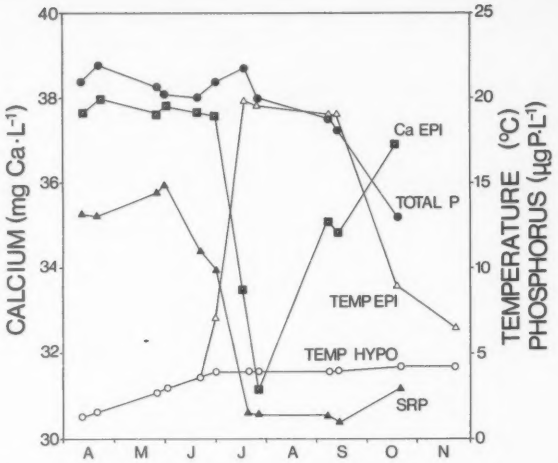

FIG. 2. Changes in calcium (■), TP (●), and SRP (▲) concentrations in the epilimnion during 1972 (IFYGL). Also shown are the epilimnetic (△) and mean hypolimnetic (○) temperatures.

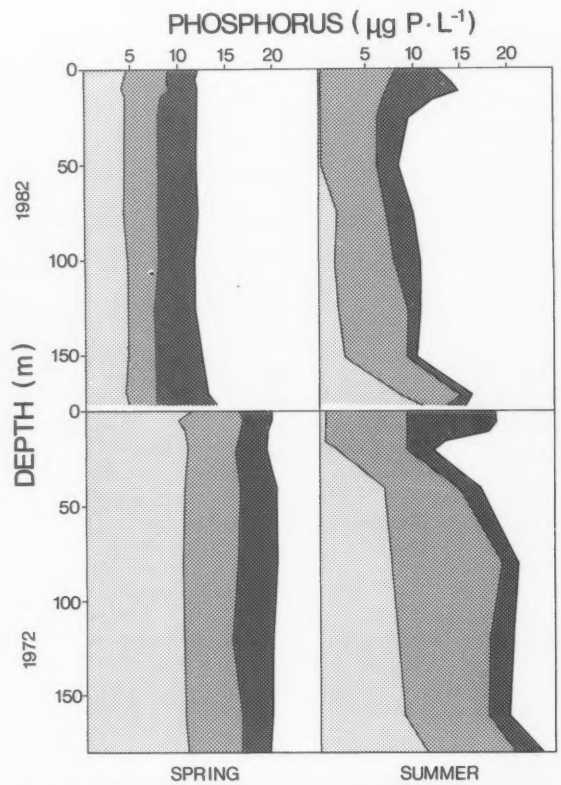

FIG. 3. Depth distribution of phosphorus (symbols as in Fig. 1) for early June (left) and mid-September (right) measured during 1982 (top) and 1972 (bottom) at the midlake station.

less than 4°C (Fig. 1). After stratification, the prevailing wind from the west caused upwelling and lower water temperatures along the north shore. Neither calm periods nor wind reversals were sufficient to modify this distribution. Generally, the epilimnion at the northshore station (401) was less than 5 m thick, but increased toward the southshore station to thicknesses

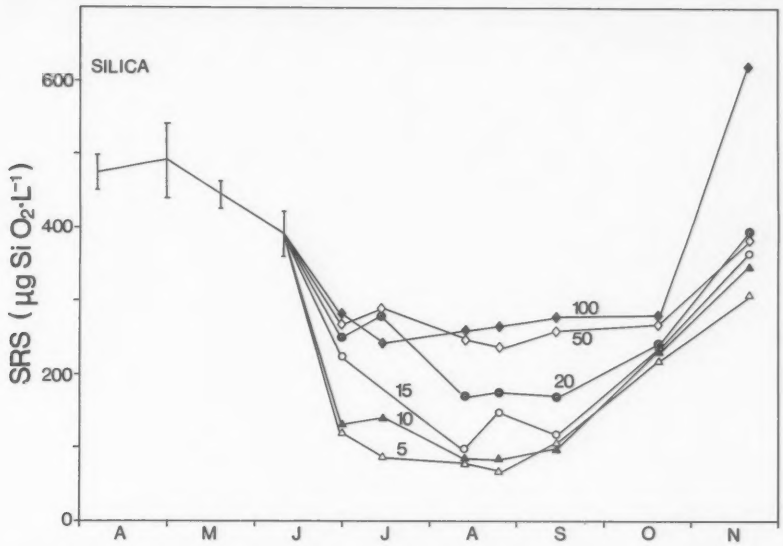

FIG. 4. Concentrations of SRS during 1982 at depths 5–100 m at station 403. Vertical bars denote range in measurements during periods of complete mixing of the water column.

of more than 20 m and were as much as 5° warmer (Simons and Schertzer 1987).

Wind can move a shallow-water column faster than a deep-water column. For this and other reasons, nearshore currents are greater than those in the midlake region. In general, currents flow along the north shore in a westerly direction, while those along the south shore flow easterly (Simons and Schertzer 1987).

Calcium

As the offshore water temperature warmed from 1.2 to 3.9°C from April to June, the calcium concentration decreased by 1 $mg \cdot L^{-1}$ (Fig. 1). With thermal stratification, the calcium concentration in the epilimnion decreased further but no increase occurred in the hypolimnion. Furthermore, the quantity collected in both deep and shallow sediment traps was similar (see below, Fig. 8). Both data sets suggest that the calcium precipitate was not resolublized in the hypolimnion. The lowest concentrations of epilimnetic calcium corresponded to maximum summer temperatures, but long before total mixing of the water column, calcium concentrations increased with fall cooling.

Coprecipitation of phosphorus with calcium carbonate is one mechanism that may reduce phosphorus concentrations in lakes (Murphy et al. 1983). Unlike most chemicals, calcium carbonate is less soluble in warm water than in cold (Stumm and Morgan 1981); however, Stabel (1986) found only a weak correlation between epilimnetic saturation indices and seasonable patterns of calcium sedimentation rates and suggested that the algae may catalyze the nucleation process. Although supersaturation is essential for precipitation, photosynthetic uptake of bicarbonate and release of hydroxide increases the pH of the microenvironment of the cell and enhances crystal formation. Our observations show that calcium carbonate precipitation followed the period of rapid temperature increase (Fig. 1) and the seasonal maximum in primary production (see below, Fig. 8). Since these events occurred at the same time, a causal relationship is not clear.

Phosphorus

Concentrations of SRP (Fig. 1) declined in June prior to calcium carbonate precipitation, leaving little SRP to coprecipitate. When currents moved a tongue of phosphorus-rich water from the southeast shore to the midlake region (Simons and Schertzer 1987), a temporary increase in total phosphorus (TP) was observed. Excluding this point, surface concentrations of TP changed little throughout the season without any measurable decline during periods of calcium carbonate precipitation. For the same reason, potential losses through coagulation of the particulate (Stabel 1986) and colloidal forms of phosphorus (Otsuki and Wetzel 1972) with calcium carbonate can also be excluded.

To determine if calcium carbonate precipitation was important in years when phosphorus and SRP values were higher, 1972 IFYGL data from a midlake station were reexamined (Fig. 2). The period of calcium precipitation coincided with a reduction in SRP from 10 to 1.5 $\mu g\ P \cdot L^{-1}$. Nevertheless, since nitrate also declined from 220 to less than 10 $\mu g\ N \cdot L^{-1}$, plankton assimilation of both SRP and nitrate was the likely explanation for the decline. As in 1982, TP showed no decline during this period; hence, we conclude that calcium carbonate precipitation has little control on phosphorus concentration in Lake Ontario.

Phosphorus spring and summer depth profiles illustrate how phosphorus cycling in Lake Ontario has changed since 1972 (Fig. 3). Spring TP concentrations have decreased from 20 to 12 $\mu g\ P \cdot L^{-1}$, while SRP changed from 10.5 to 4.5 $\mu g\ P \cdot L^{-1}$. Soluble unreactive phosphate (SUP) was also less in 1982, but particulate phosphorus has not changed. Summer values illustrate that SRP was depleted in the epilimnion in both years, but below 15 m, values were higher in 1972 whereas metalimnetic

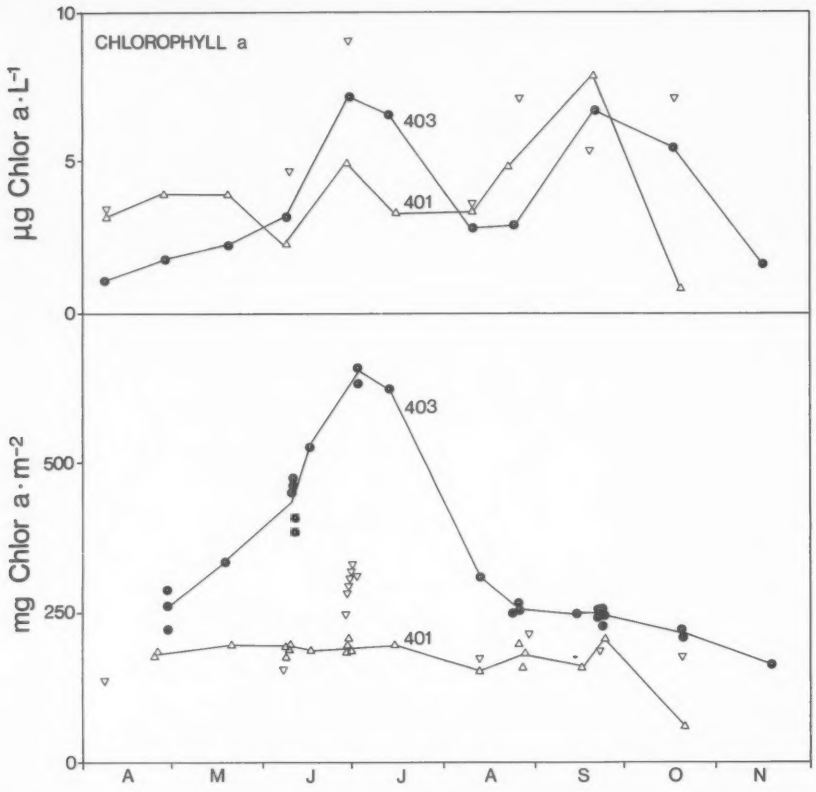

FIG. 5. Concentrations of chlorophyll *a* (uncorrected) for stations 401 (△), 403 (●), and 405 (▽) from 5 m (top) and on an areal basis throughout the water column (bottom).

SRP concentrations in 1982 remained low (<2 μg $P \cdot L^{-1}$) even to 50 m. Upwelled water would not bring any significant quantity of SRP to the trophogenic zone in 1982, but as illustrated by the October upwelling event in 1972 (Stadelmann and Fraser 1974), this was previously an important mechanism for phosphorus recycling.

As in most lakes, epilimnetic phosphorus concentrations decreased over the summer in 1972, but recently they have increased (Fig. 1, 2; and Stevens and Neilson 1987), and by midsummer, epilimnetic concentrations exceeded those in the hypolimnion. The Niagara River, the major phosphorus load to Lake Ontario, has TP concentrations lower than the lake itself (Nielson and Stevens 1987) and in effect serves to dilute the phosphorus in the lake. It remains unexplained how phosphorus is being pumped to the surface zone at a rate in excess of that lost due to sedimentation.

Reactive Silica

All phytoplankton have a silica requirement for protein and carbohydrate synthesis, but only among the diatom and chrysophyte genera does silica become ecologically important (Reynolds 1984). The onset of stratification is one of the critical factors which sets up the sequence of events that determine the summer biomass and nutrient depletion processes in lakes such as Ontario and Michigan (Scavia and Fahnenstiel 1987). Even before the thermal bar had developed, diatom growth was well underway (Gray 1987). Consistent with the view of Margalef (1978) and Schlesinger et al. (1981), diatom growth was favored by the cold temperatures, higher nutrient content, and turbulent conditions. During summer, diatom growth continued only along the north shore where current velocities were high and upwelling events occurred. At southshore station 405, however, there were few diatoms (Gray 1987).

While most algae were eaten or decomposed before leaving the metalimnion, diatoms were observed sinking throughout the water column weeks after stratification (I. M. Gray and F. R. Pick, unpubl. data). In the sediments, the high lipid content of the diatoms provides essential nutrition for a healthy benthos community (Gardner et al. 1985). A decline in diatom production through SRS deficiency could alter the entire lake ecosystem.

In summer, SRS concentrations at station 403 fell to about 80 μg $SiO_2 \cdot L^{-1}$ (Fig. 4) in 1982, but values in 1972 were even lower. Depletion of SRS occurred only in the top 15 m, so upwelling events would bring SRS back into the trophogenic zone. This may explain why summer diatom growth is associated with the north shore rather than at the downwelling south shore. As with calcium (Fig. 1), the SRS concentration in the surface waters increased after 24 August (Fig. 4) long before the period of fall mixing. No total silica budget is available for Lake Ontario at this time, so the source of the SRS increase in the water column remains poorly defined.

According to Schelske et al. (1983) and Stoermer et al. (1985), phosphorus loading increased in Lake Ontario follow-

TABLE 1. Comparison of measured POC with carbon estimated from enumerations of the various components of the plankton, stations 401 and 403.

	9 June		13, 15 July		24 August		23 September	
	401	403	401	403	401	403	401	403
Wet weight ($\mu g \cdot L^{-1}$)								
Bacteria[a]	288	101	160	126	286	283	388	263
Phytoplankton[b]	1692	699	3114	1184	980	1182	2742	1538
Ciliates[c]	238	24	155	43	165	69	113	102
Zooplankton[d]	100	120	175	340	330	310	450	430
Total	2318	944	3604	1693	1761	1844	3693	2335
Total carbon[e]	229	93	357	167	174	182	356	231
POC	328	163	504	564	457	408	555	537
Percent enumerated	70	57	71	30	38	45	66	43

[a]Pick and Caron (1987).
[b]Data summed from Pick and Caron (1987), including heterotrophic flagellates, and from Gray (1987).
[c]Taylor and Heynen (1987).
[d]Taylor et al. (1987).
[e]Conversion factors from Healey (1975).

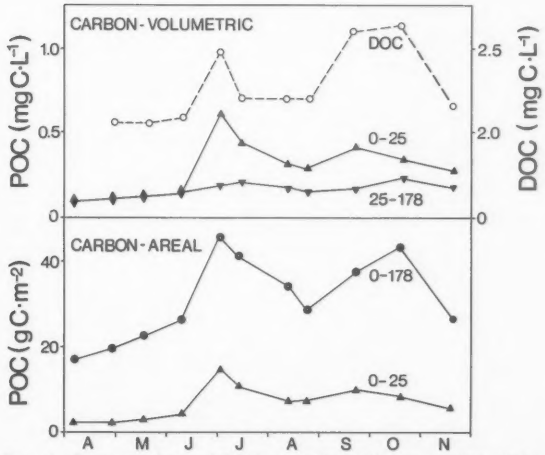

FIG. 6. Concentrations of POC at station 403, averaged at depths between 0 and 25 m and 25 and 178 m (top) and integrated throughout the water column and from surface to 25m (bottom). Also shown is the DOC concentration throughout the season.

ing early settlement and forest clearance. This resulted in storage of silica in sediments such that after 1850, diatom growth in Lake Ontario was silica deficient. Unless Lake Erie was also silica deficient, the residence time of Lake Ontario is too low for these arguments to be valid. Our observations suggest that when physical conditions were appropriate, diatoms were present.

Chlorophyll

A diphasic pattern for chlorophyll *a* concentration, typically found in oligotrophic lakes, was observed at the midlake station (Fig. 5). During thermal bar conditions, chlorophyll *a* concentrations increased at both nearshore stations to twice that at the midlake station. After stratification, chlorophyll *a* concentrations peaked at 403, declining through an August "clear water phase" (Sommer et al. 1986) and then increasing to a fall peak in September before declining through October and November.

On an areal basis the seasonal chlorophyll *a* pattern (Fig. 5) is not diphasic but follows the seasonal pattern for solar radiation. Prior to the end of June at 403, chlorophyll *a* was evenly dispersed throughout the water column during the period of deep mixing. Consequently, integrated values were greater than at the warmer nearshore stations. Peak values occurred on 2 July at 403 and then declined without any fall peak. In contrast, at nearshore stations 401 and 405 the areal chlorophyll *a* concentration remained fairly constant throughout the season.

Margalef (1978) calculated that 99% of incident light could be trapped by about 300 mg chlorophyll $a \cdot m^{-2}$ but thought that this would be rarely achieved and expected values of 5–100 $mg \cdot m^{-2}$ to be commonly found. Our values were as high as 500 $mg \cdot m^{-2}$. However, only in the upper 25 m was light effectively harvested. Here, areal chlorophyll *a* values ranged from 50 to 150 $mg \cdot m^{-2}$.

The physical transport of Lake Ontario water masses control the algal biomass when the depth of the mixing zone exceeds the depth of the euphotic zone. Under such conditions, nutrient control of algal growth cannot be important and may explain, in part, why Stevens and Neilson (1987) found no significant reduction in chlorophyll *a* with reduced phosphorus concentration. It should be noted, however, that a metalimnetic chlorophyll *a* maxima was a common feature of the 1972 depth profiles (Dobson 1984), but these were not observed in 1982. In the intervening years, monitoring programs used a 0- to 20-m composite sample and such peaks could not be observed. Perhaps a major change in chlorophyll *a* has occurred in Lake Ontario at a depth not routinely monitored.

Particulate Organic Carbon

The seasonal pattern of POC (Fig. 6) in the surface waters at station 403 has similar features to that for chlorophyll *a* (Fig. 5), and a significant correlation exists between both parameters at all stations (Pick 1987). However, the fall peak in POC concentration was less pronounced than that for chlorophyll *a*.

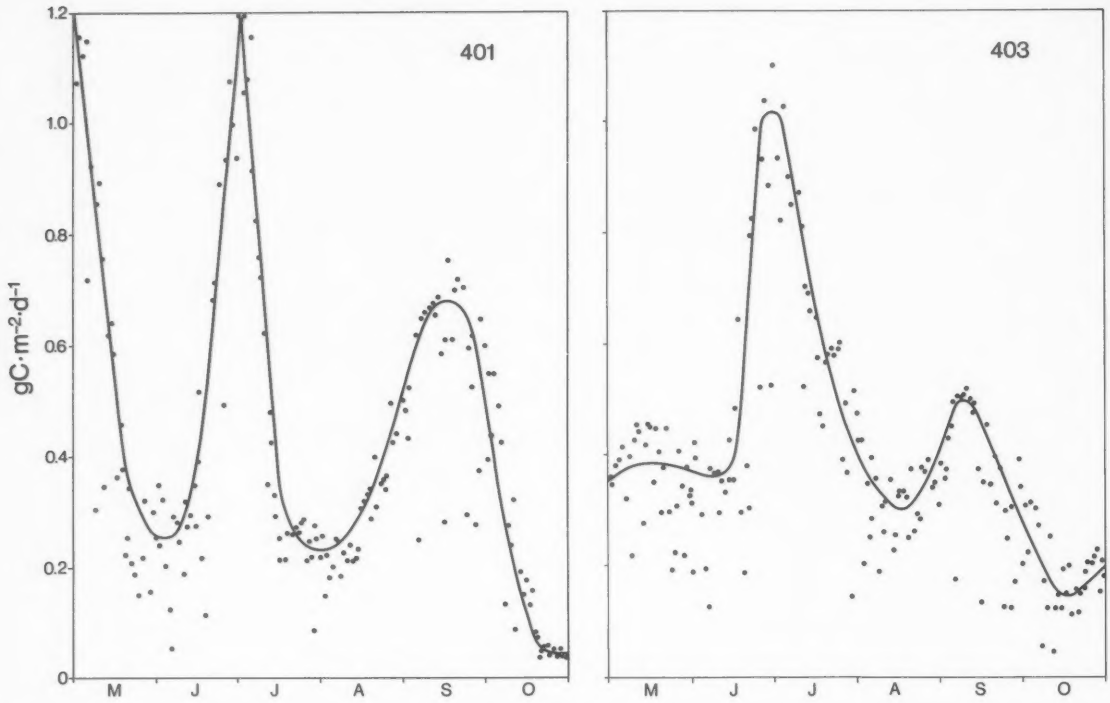

FIG. 7. Computer-calculated values for daily integral primary production for stations 401 and 403 based on bimonthly photosynthesis irradiance measurements on water samples collected from 5 m.

Furthermore, areal POC doubled through the year whereas areal chlorophyll *a* declined after early July. These observations illustrate that POC and chlorophyll *a* each provide important, but different information. When particulate chlorophyll is degraded, it is no longer chlorophyll, but when POC is transformed or degraded, it is either still POC, DOC, or is respired as carbon dioxide.

Throughout the year, epilimnetic POC represents less than 25% of the POC in the water column. DOC concentrations are four to seven times the summer POC. In small lakes of similar trophic state the effect of the drainage basin would be more important, but the DOC concentrations are similar to those in Lake Ontario. This suggests that much of the DOC is produced within the lake, but its source, fate, and turnover time remain unknown.

From microscopic enumeration of the components of the plankton, the percent carbon accounted for in live organisms ranged from 30 to 71% of the POC (Table 1). The lowest percent was found at the midlake station even though here, detrital interference of POC was minimal (Pick 1987). As phytoplankton become nutrient stressed the amount of fibrillar organic material increases on the surface of many of the microorganisms (Leppard et al. 1977). This may further explain some of the differences observed during the phosphorus deficient time of the year (Lean et al. 1987). Despite the fact that sediment resuspension occurred more frequently at the nearshore station (Rosa 1985), when we subtract the estimated detrital interference (113 $\mu g\ C \cdot L^{-1}$), we come close to identifying all POC as living organisms. Previous workers have concluded that living organisms account for less than 30% of the particulate matter in lakes (Wetzel 1983). With the improved techniques to measure picoplankton and microzooplankton biomass, the undetected fraction, termed "detritus," becomes smaller.

Primary Production

Integral primary productivity (Fig. 7) was higher at 401 during thermal bar conditions, but otherwise, both stations were similar and patterns followed that for chlorophyll *a*. Maximum rates for primary production were reached soon after lake stratification. This also corresponded to maximum chlorophyll *a* concentration (Fig. 5). Rates of primary production declined through July but increased in August before declining again through the fall period.

It should be noted that Fee's (1984) model only integrates production during the light period and does not inlcude losses during the night. Cuhel and Lean (1987) found that nightime losses of fixed carbon were proportional (10–20%) to carbon fixed during the light period. This was due in part to losses in low molecular weight and carbohydrate biopolymers as nighttime protein synthesis continued at daytime rates. Clearly, modifications in Fee's model are necessary to account for nighttime losses of fixed carbon, but as will be shown below, much more serious problems exist in our attempts to balance carbon production with losses.

Sedimentation

Turbulent conditions of the nearshore zone cause sediment resuspension and make sediment trap data for this zone difficult

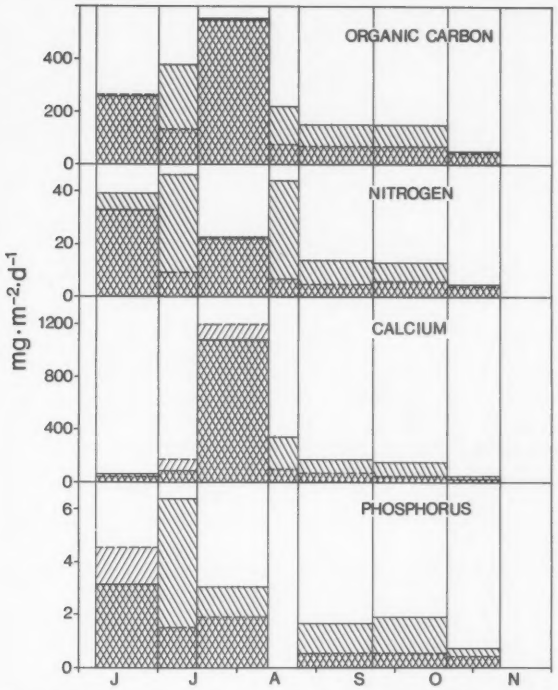

FIG. 8. Sedimentation rates for carbon, nitrogen, calcium, and phosphorus. In most cases, areal sedimentation rates were higher in traps at 176 m ▨ than in those at 40 m ▨.

to interpret (Rosa 1985). To minimize problems of sediment resuspension, we measured sedimentation rates at the midlake station (Fig. 8). Calcium carbonate precipitation was restricted to early July (Fig. 1) and was highest in sediment traps deployed between 15 July and 11 August (Fig. 8) but otherwise cannot be used to explain the elevated ash content of sedimenting nutrient (Zimmermann et al. 1987). Since the percent ash was approximately 90% in sediments, 70% for sediment trap material, but only 15-30% for seston (Zimmermann et al. 1987), we must conclude that even at the midlake station, a considerable portion of the sediment trap material was resuspended sediments (Charlton 1983).

Carbon sedimentation rates were similar for traps located at both 40 and 176 m. If decomposition occurred in the water column, the deep traps should have collected less carbon than the 40-m traps. Instead, they collected at least as much. Traditionally, it was thought that as POC settled to the bottom, "mineralization" by bacteria would release nutrients into the water column, increasing phosphorus and SRP in the hypolimnion. Observed values (Fig. 3) for phosphorus do not support this hypothesis. As in Lake Lucerne, where Gachter and Mares (1985) observed that the phosphorus content of organic material increased during sedimentation, our deep traps collected more phosphorus than the shallow traps (Fig. 8). This shows that either settling material actually removed phosphorus from the water column or the increase in deep traps was simply due to resuspension.

Phosphorus sedimentation rates, measured at 40 m during the summer period, were generally less than 1 mg $P \cdot m^{-2} d^{-1}$. This amount represents only 0.2% of the phosphorus in the upper

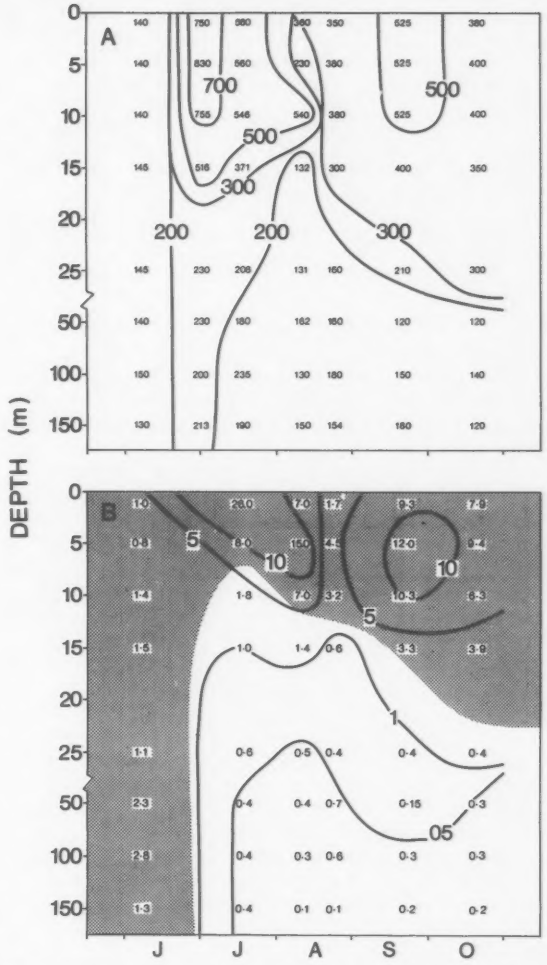

FIG. 9. Depth distribution of POC ($\mu g\ C \cdot L^{-1}$) (top) from June to October in 1982 and depth distribution of zooplankton (>64 μm) grazing ($\% \cdot d^{-1}$) (bottom). Shaded area indicates mixing depth.

40 m. In other words, a quantity equivalent to that in the upper 40 m would be lost through sedimentation every 500 d! This supports the conclusion that phosphorus is effectively recycled in the trophogenic zone during the summer period. Corrections for sediment resuspension would only lower the sedimentation rate estimate. Effective recyling of nitrogen also occurs in the upper 40 m, for summer nitrogen sedimentation rate of 6 mg $N \cdot m^{-2} d^{-1}$ can be converted to a loss rate constant of only $0.1\% \cdot d^{-1}$.

Phosphorus sedimentation rates were not unusually high during the period of high calcium sedimentation. This observation is consistent with the conclusion reached in the section on phosphorus cycling (above) that coprecipitation of phosphorus with calcium carbonate is not a significant phosphorus loss process.

Zooplankton Grazing

Prior to summer stratification, zooplankton community filtration rates were only $1–2\% \cdot d^{-1}$ throughout the entire water

TABLE 2. Net changes in areal POC over the entire water column (0–178 m) compared with carbon production rates and lost through sedimentation and zooplankton grazing. Numbers in parentheses are daily rates. Units are g $C \cdot m^{-2} \cdot d^{-1}$.

Period	Days	Production	Sedimentation	Net change	Grazing
7 June – 30 June	23	16.1 (0.70)	6.1 (0.26)	+14.1 (0.63)	11.3 (0.49)
30 June – 14 July	14	10.5 (0.75)	5.3 (0.38)	−4.0 (0.29)	8.4 (0.61)
14 July – 12 Aug.	29	13.1 (0.45)	16.0 (0.55)	−7.5 (0.26)	21.1 (0.73)
12 Aug. – 23 Aug.	11	3.6 (0.33)	2.3 (0.21)	−5.6 (0.51)	5.3 (0.49)
23 Aug. – 22 Sept.	30	12.0 (0.40)	4.5 (0.15)	+8.3 (0.28)	8.6 (0.29)
22 Sept. – 20 Oct.	30	9.0 (0.30)	4.4 (0.15)	+7.8 (0.26)	25.4 (0.85)
28 Oct. – 10 Nov.	21	5.3 (0.25)	1.0 (0.05)	−17.0 (0.81)	12.8 (0.61)
Total	158	69.6	39.2	−3.9	87.4

column (Fig. 9). In other words, using the rate measured for 10 min, a value of 1–2% of the lake volume would be filtered free of particles similar to the labeled food (*Chlorella*). With stratification, grazing activity was confined to the upper mixed zone. (Only included were rates obtained by collecting animals on a 64-μm Nitex net. Not included were results where the filtrate through 64 μm was also passed through a 30 μm net where rotifers and other small zooplankton accounted for filtering rates of an additional 1–2% $\cdot d^{-1}$. Further experiments with yeast and bacteria usually gave comparable results but will be published elsewhere.)

Areal grazing rates were calculated by multiplying the filtering rate by the POC concentration and integrating over depth (Table 2). Since the POC in particles less than 30 μm was 70–90% of the total POC, an error of 10–30% may result from using total POC as available food. Zooplankton grazing experiments were conducted only on specific dates but were extended to periods that corresponded to that for deployment of sediment traps. Primary productivity measurements were also integrated over the same time intervals (Table 2). Zooplankton grazing exceeded integral production (not corrected for nighttime losses) by 30%. Furthermore, an amount equivalent to 58% of the primary productivity was collected in sediment traps.

Using different methods, Scavia et al. (1986) also found that losses exceeded production in Lake Michigan. One difference between the studies was that Scavia et al. (1986) thought that prior to stratification, sedimentation was more important than zooplankton grazing. They did not consider that grazing activity extends throughout the water column prior to stratification. On an areal basis, zooplankton grazing is the most significant sink for carbon both prior to stratification and during the summer (Table 2).

With stratification, as the POC concentration increased in the surface waters (Fig. 6 and upper panel of Fig. 9), zooplankton filtration rates also increased to a maximum value of 26% $\cdot d^{-1}$ before a clearwater phase (discussed for other lakes by Lampert et al (1986) and Sommer et al. (1986). This was followed by a decline in zooplankton biomass (Taylor et al. 1987) and filtering rate (Fig. 9). A similar pattern in Lake Michigan was attributed to calcium carbonate precipitation (Scavia et al. 1986). While the sequence of events was similar in Lake Ontario, it is not known whether the precipitation of calcium carbonate was the cause of the zooplankton crash or simply a coincidence. The hypothesis that zooplankton biomass declined through starvation should also be tested by using egg ratios or lipid content.

After stratification, the grazing activity was highest in the upper mixed zone. Rates in the deeper strata were usually less than 1% $\cdot d^{-1}$. Filtration rate plotted as a function of POC (data from Fig. 9) showed that below POC concentrations of approximately 400 μg $\cdot L^{-1}$ the filtration rate was near 1% $\cdot d^{-1}$ but increased rapidly above POC concentrations of 500 μg $C \cdot L^{-1}$. Where there was food, zooplankton grazing activity was highest.

It appears that zooplankton grazing exceeds carbon produced through photosynthesis. Using only POC less than 30 μm would improve the balance between grazing and production. If about half the carbon injested was released and ultimately settled out, a balance between production and losses would be achieved (Table 2).

Based on respiration measurements in Lake Washington, Duvol (1979) considered that zooplankton consumed an amount of carbon equivalent to carbon produced. Scavia et al. (1986) found that summer water column bacterial carbon demand exceeded the potential supply produced autotrophically during that period and suggested that temporal and spatial disequilibrium of labile organic carbon supply and bacterial use was responsible. Such observations were also made by Williams (1981) in a marine ecosystem. He thought either that the production was too low, the grazing rate too high, or as a result of incomplete understanding of the community structure that the calculations were not being done correctly.

Williams (1981) calculated that up to 65% of the primary production was recycled through the heterotrophic community. One pathway involved excretion of DOC by autotrophs followed by reutilization by bacteria. Such rates are commonly measured by acidification and bubbling lake water following filtration through 0.2-μm filters after incubation with ^{14}C-labeled bicarbonate. In Lake Ontario, excretion rates were less than 1% of primary production. While there is activity in the 0.2–1.0 μm size class (Lean et al. 1987), this can be explained by direct assimilation of ^{14}C-labeled bicarbonate by autotrophic picoplankton (Caron et al. 1985b) rather than reutilization of algal-excreted DOC by bacteria.

Grazing by heterotrophic flagellates on heterotrophic bacteria is another means by which carbon can be recycled into the food chain (Williams 1981). Growth rates of bacteria result in doubling times every 8 h at summer temperatures in Lake Michigan (Scavia et al. 1986). Pick and Caron (1987) showed that numbers were correlated with temperature. They are so efficient at taking up phosphate during phosphorus-deficient conditions (Lean et al. 1987) that it is unlikely that they are ever phosphorus deficient. Filtering rates for heterotrophic flagellates similar to those in Lake Ontario (Pick and Caron 1987) are

1×10^{-5} to 2×10^{-5} mL·h^{-1} (Anderson and Fenchel 1985). A clearance rate for peak numbers (10^3·mL^{-1}) of these organisms would be 36%·d^{-1}.

Using the filtration rates cited above, an estimate of the carbon flux through heterotrophic flagellates in Lake Ontario is approximately 40 mg C·m^{-2}d^{-1} during periods of peak abundance. This assumes that POC in the 0.2–1.0 μm fraction is the food for these organisms and that our measurements of 10–20% of the total POC are correct. This quantity is at least half autotrophic production and should be much more carefully studied. At present we are unsure of the source of the carbon for the heterotrophic community.

Phosphorus Regeneration

The above carbon budget provides information which must be considered in light of mechanisms for phosphorus regeneration. Traditionally, bacteria were thought to regenerate nutrients, but in fact in Lake Ontario they are users of phosphorus (Lean et al. 1987). Caron et al. (1985a) showed that bacteria alone were not responsible for nutrient regeneration but required the presence of microflagellates to be effective.

Heterotrophic flagellates, however, have a high assimilation efficiency (Calow 1977) and consequently at low particulate C:P ratios may regenerate little of the phosphorus they ingest. Olsen et al. (1986a) showed that when C:P ratios were above 120, all phosphorus ingested by zooplankton was needed for growth and reproduction. Under such conditions, no release of phosphorus can be expected. In Lake Ontario in July, particulate C:P ratios were greater than 120 (Fig. 1, 9), so little zooplankton regeneration of phosphorus would occur at this time. However, since most zooplankton are eaten by planktivorous fish with a lower assimilation efficiency, nutrient regeneration is achieved. In low-phosphorus habitats, longer food chains result in more efficient nutrient regeneration. We must now accept that bacteria and zooplankton also utilize SRP under certain conditions and that most of the so-called decomposition occurring in the water column results from nutrient regeneration, not only by herbivores but also at higher trophic levels.

Existing technology is sufficient to direct our attention to gaps in our knowledge of ecosystem processes. The common currency of aquatic ecosystems is organic carbon, yet we are presently unsure of our estimates for production and even less sure of its fate. Our data suggest that zooplankton consume most of the primary production and that an amount equal to about half of the primary productivity settles out of the water column. Superimposed on this classic trophodynamic concept is the activity of the heterotrophic flagellates which are capable of filtering one third of the surface waters free of bacteria each day. The integration of physical (light, temperature, and mixing) and chemical (phosphorus, nitrogen, calcium, and silica) factors results in partial understanding of the life support system for lakes, yet further improvement in our ability to measure the significant carbon fluxes is required.

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